REPRODUCTIVE STRUCTURE OF LITHOCARPUS SENSU LATO (FAGACEAE): CYMULES AND FRUITS

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Seventy-three species were examined for structural and developmental details of the cymules and fruits. The cymules bear one to seven or more flowers and are subtended by one to nine or more bracteoles. Generally, the number of flowers and bracteoles in the pistillate cymules is the same or less than in the staminate ones. Some of the latter have an inner set of bracteoles that could be homologous to the pistillate cupule. Scales are present at anthesis on the cupules of all species examined, but in some species they fail to enlarge, are torn or disintegrate, or fall away as the cupule matures, leaving the cupule essentially naked. In species with scaly cupules at maturity, the scales enlarge and sometimes also become adpressed, thickened, or elongated. Some cupules are intermediate between the naked and scaly ones. Apparently adventitious flowers borne on the outer walls of some cupules are often abortive flowers of the same cymule that have been elevated by the maturing cupule of the fertile flower, but in some cases they could be developed from latent primordia that are axillary to the cupular scales.

Nearly all that is known of the reproductive structure of *Lithocarpus* Blume comes from studies done for taxonomic purposes. Most notable are the contributions of Camus (1948, 1952–1954) and Soepadmo (1968, 1970, 1972), which contain numerous illustrations and some discussion of reproductive structure and its possible phylogeny. Hjelmqvist (1948) detailed floral and cymular structure in several species and provided some phylogenetic assessments. Nevertheless, only a few species have been investigated for reproductive detail, and no comprehensive overview of the genus is available. Here I report on morphological, developmental, and evolutionary aspects of partial inflorescences (cymules) and fruits in 73 species that represent eight of the 14 subgenera proposed by Camus (1952–1954). I give particular attention to the organization of the cymules and cupules. Details of floral structure will be presented elsewhere.

Lithocarpus, with perhaps 300 species when taken in its broadest sense, is second in the Fagaceae only to *Quercus* L. in number of species. The genus ranges from northeastern India across central China to Korea and southern Japan, south to southeastern Asia, the Philippines, and the East Indies as far east as New Guinea. There is one American species, *L. densiflora,* which occurs in the coastal mountains from Douglas County, Oregon, south to Ventura

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County, California, and at scattered locations in the Sierra Nevada of California (Little, 1971). The range of the genus is almost exactly congruent with that of the third largest genus of Fagaceae, *Castanopsis* (D. Don) Spach, but it is much less than that of *Quercus.*

Lithocarpus is found on a variety of soil types from sea level to about 4000 m, but it is most abundant at middle elevations, where it is sometimes one of the dominant forest genera, often with *Quercus* and members of the Lauraceae.

Some taxonomists (e.g., Barnett, 1940, 1944; Camus, 1952–1954; Soepadmo, 1972) have recognized *Lithocarpus* in the broad sense, but others (e.g., Li, 1963; Lin & Liu, 1965; Liao, 1969) have preferred to restrict that name to some species and to place others in segregate genera. Those favoring the broad interpretation justify their position by noting that there are intermediate species between the groups. Further taxonomic complications arise from the fact that certain species are intermediate in many respects between *Lithocarpus* s.l. and both *Castanopsis* and *Quercus.*

Camus (1952–1954) recognized 14 subgenera in *Lithocarpus,* most of them with fewer than 15 species. Because her subgeneric classification covers the entire genus in its broadest sense, it is the basis of reference for the work presented here. Soepadmo (1970, 1972), in his treatment of *Lithocarpus* for the *Flora Malesiana,* described some new species and reduced or did not accept some of Camus's species; of the 136 species recognized by Camus for Malesia, he accepted only 64 as good species but did not assign them to subgenera. His nomenclature is used for the southeastern Asian species discussed here.

The classification of *Lithocarpus* is based mostly upon cupule and fruit characters (Barnett, 1940, 1942, 1944; Camus, 1952–1954; Li, 1963; Lin & Liu, 1965; Liao, 1969; Soepadmo, 1970, 1972), as it is in other Fagaceae. Gross inflorescence and flower characters are useful in separating genera (Soepadmo, 1970; Kaul & Abbe, 1984) but not in distinguishing species.

Camus (1952–1954) believed *Lithocarpus* to be one of the most primitive members of the family. She cited seven reproductive characters as primitive (but was not clear about the reasons for those assessments): the abortive ovules apical in the nut (known elsewhere only in *Quercus* subg. *Cyclobalanopsis* and one section of subg. *Quercus*); the scar of the nut large in some species; the cupule asymmetric in some species; the tomentum that lines the cupule dense (known elsewhere only in *Quercus* subg. *Cyclobalanopsis* and some sections of subg. *Quercus*); the cupule poorly developed at anthesis, as is also the case in *Quercus*; the cupule fused for much or all of its length to the nut in some species; and the partitions of the nut absent or poorly developed in some species. Schottky (1912) and Hjelmqvist (1948) believed *Lithocarpus* to be the most primitive genus of the family, and they suggested that it gave rise—or is a sister group—to *Quercus* s.s. and *Cyclobalanopsis* (*Quercus* s.l. subg. *Quercus* and subg. *Cyclobalanopsis,* respectively). Forman (1966; see also Elias, 1971), however, postulated separate origins of *Quercus* and *Lithocarpus* from hypothetical ancestors and thus implied morphological parallelisms of the two; *Trigonobalanus* Forman was seen as having some intermediate characteristics.

Camus (1952–1954, p. 1188) also noted the "affinités indéniables" of *Lithocarpus* subg. *Cyclobalanus* with *Quercus* subg. *Cyclobalanopsis.* Both have more than three styles per flower in many instances, annular cupules, apical abortive ovules, rudimentary perianthopodia in some instances, and entire, evergreen leaves. The stigmas, styles, and stamens of each subgenus are typical of their genera, however, and their characteristics are not shared by the two subgenera. It is mostly because of these distinct floral characteristics that Barnett (1940), Camus (1952–1954), and Soepadmo (1968, 1970, 1972) maintained *Lithocarpus* distinct from *Quercus* despite the similarities in fruits and cupules. I have shown all these and other differences between the two genera elsewhere (Kaul, 1985, *t. 2*).

The cupules of *Lithocarpus* and *Quercus* are often indistinguishable, but those of *Lithocarpus* have a greater variety of shapes and ornamentation. Further, although there is a rather sharp distinction between the lamellate cupules of *Quercus* subg. *Cyclobalanopsis* and the scaly ones of subg. *Quercus,* in some species of *Lithocarpus* there are intermediate cupular patterns.

Further complications to generic delimitation of *Lithocarpus* arise when some of the species that strongly suggest *Castanopsis* sect. *Pseudopasania* are examined. These were placed in *Lithocarpus* subg. *Pseudocastanopsis* by Camus (1952–1954) and resemble *Castanopsis* because of cupular and foliar similarities (i.e., the scales in three groups, the castanopsoid hairs on the abaxial leaf surface, and the cupules of *L. fissa* opening by three valves). Soepadmo (1970) noted several differences between the two genera: *Castanopsis* has the inner bark surface smooth, the wood rays only uniseriate, and the cupules solitary (but enclosing one to three nuts). The cupule has a definite number of growing points separated by vertical rows of scales, and its vascular system shows a dichasial pattern. *Lithocarpus* has the inner bark surface longitudinally ridged, the wood rays both uni- and multiseriate, the cupules solitary or clustered and each enclosing a single nut, and the cupular vascular system not dichasial. The cupule has a continuous, circular growing edge, and there are no sutures.

Barnett (1940) believed that *Lithocarpus* and *Castanopsis* are very close and that their separation is perhaps more artificial than natural. Nevertheless, she believed their fruit structure distinct enough to treat the two as genera. She noted that in species of *Lithocarpus* with spiny cupules (e.g., *L. garrettiana, L. lappacea, L. longispina, L. recurvata*), the spines are certainly recurved scales. The spines and tubercles of *Castanopsis,* however, do not appear to be the original cupular scales but develop later, often in the axils of the original scales. She included in *Lithocarpus* those species with oblique cupular lamellae, whether tuberculate or not, in which the fruit is oblique (e.g., *L. blumeana, L. encleisacarpa*). She placed *C. acuminatissima* in *Castanopsis,* however, because it has oblique cupules with irregular whorls of short spines or tubercles and because it has some castanopsoid anatomical characters.

In *Lithocarpus* each pistillate flower has its own cupule (as is the case in *Quercus*), but sometimes the cupules are grouped and even fused. In extreme cases of fusion, the combined cupules appear almost as a single cupule enclosing several nuts. Soepadmo (1970) showed that in organization of the vascular system of the cupule, *Lithocarpus* is the same as *Quercus* but markedly different from *Castanopsis.* Where adjacent cupules are fused, the unified wall that separates the flowers retains the separate vasculature of each cupule.

Forman (1966) interpreted the one-flowered cupule of *Lithocarpus* as being derived from a three-flowered cymule whose valves fused to form one cupule around each flower; the one-flowered cupule of *Quercus* became so by loss of some valves and the lateral flowers. Thus the one-flowered cupules of both genera were seen as convergently evolved. This interpretation was illustrated by Elias (1971).

Camus (1952–1954) and Soepadmo (1970) noted the variety of patterns of cupular fusion to the nut. In some subgenera the mature cupule entirely encloses the nut and is totally fused to it for its entire length (subg. *Oerstedia,* some sections of subg. *Lithocarpus*); in others the cupule entirely covers the nut but is only partially fused to it (subgenera *Lithocarpus* (sect. *Costatae*), *Pachybalanus, Synaedrys*) or is not fused except for the basal scar (subg. *Pseudosynaedrys,* and some species of subgenera *Pasania* and *Pseudocastanopsis*). In the unique subgenus *Corylopasania* the cupule not only encloses the nut but also is much prolonged beyond it into a narrow tube; the cupule is only basally fused to the nut. In many taxa (subgenera *Cyrtobalanus* and *Gymnobalanus,* as well as many species of subgenera *Cyclobalanus* and *Pasania*) the cupule covers just part of the nut and is not fused to it but the basal scar is large. Camus believed that the greater degree of fusion is the more primitive condition in the genus.

In some species of *Lithocarpus* the cotyledons are free, but in others they are fused. The latter condition is found in some species of *Quercus,* too, and Nixon (1985) considered it to be the derived condition in that genus. The endocarp is tomentose in many species, as it is in some members of *Quercus.*

MATERIALS AND METHODS

I have examined more than 1000 specimens that my colleagues and I collected in Asiatic and southwestern Pacific island forests. We took special care to collect developmental as well as mature material. Most of the specimens were identified by E. Soepadmo, the most recent monographer of southeastern Asiatic *Lithocarpus* (Soepadmo, 1970, 1972) and by other taxonomists residing in the areas of provenance of the specimens.

Most of the specimens were stored in FAA, quinoline-sulfate solution, or glycerin-alcohol. All are documented by dried voucher specimens in my collection, for which various sets of duplicates are deposited in A, BH, G, K, L, MIN, SING, and US.

OBSERVATIONS

Gross Structure of the Inflorescences

The overall structure of the inflorescences of *Lithocarpus* has been dealt with in some detail (Kaul & Abbe, 1984; Kaul, 1986). The genus was shown to have the most elaborate gross inflorescence structure among *Lithocarpus, Castanopsis, Castanea,* and *Quercus.* It was suggested that this elaborate structure is the least specialized condition—one that gave rise to more advanced inflorescences by loss of branching and separation of staminate from pistillate flowers first within the spike and ultimately, in *Quercus,* into separate spikes.

Spikes bearing usually sessile cymules are variously aggregated into reproductive branches that are caducous or persistent. In a few species some spikes, especially the staminate ones but occasionally the pistillate as well, are branched at a cymule (Kaul, 1986). The spikes are variously entirely staminate, entirely pistillate, androgynous, or androgynecandrous, and more than one pattern often occurs on a given tree. Furthermore, some cymules contain various combinations of staminate, pistillate, or perfect flowers (see Kaul & Abbe, 1984, *fig. 4*). Those cymules at the transition point on a spike between staminate and pistillate cymules more often have both flower sexes or perfect flowers than do more proximal or distal cymules. Within a spike, the pistillate flowers are more likely to occur proximally than distally, but the spikes bearing pistillate flowers are more abundant distally in the total spike-bearing shoot system. In a few instances the staminate and pistillate cymules are mixed for short distances along the spike. These phenomena are illustrated in the papers cited above, while details of cymule and fruit structure are emphasized here. There is much infraspecific variability in reproductive structure both locally and throughout the ranges of the species, and variant morphological patterns are likely to be found in specimens of the species illustrated here that are collected from other parts of their ranges.

Cymules in Lithocarpus

The groups of flowers spaced along a spike are often called cymules, dichasia, or partial inflorescences. "Cymule" is used here generally for the presumably condensed pleiochasia and dichasia that characterize *Lithocarpus* and other Fagaceae.

In the specimens examined for this study, the number of flowers in a cymule ranged from one to seven (or more in a few instances), but one, three, and five were the usual numbers (Table). (Downward departures from the typical numbers are common in a few cymules at the extreme proximal and distal ends of a spike in most species; such exceptions are not included in the data presented here.) Often the staminate and pistillate cymules on a specimen contain the same number of flowers (this was true for 29 of the 73 species shown in the Table), and where the number of flowers is variable and rather high in the staminate cymules it is also that way in the pistillate cymules (e.g., *Lithocarpus elegans* and *L. harmandii,* Table). However, the number of flowers in a pistillate cymule never exceeds that in the staminate cymules on the same plant and, in fact, is frequently lower (see Table). There is some variability in cymule flower number from tree to tree and even from branch to branch within some species (e.g., *L. celebica, L. dealbata, L. fenestrata, L. harlandii, L. lucida, L. reinwardtii,* and *L. sootepensis*).

In most cases all the flowers of a staminate cymule are fully formed at anthesis. Only occasionally do clearly abortive flowers appear, as in *Lithocarpus buddii,* where the central (uppermost) flower is fully developed but the two lateral ones are abortive. Likewise, all the flowers of the pistillate cymules are usually nonabortive at anthesis, but many of them abort later due to apparent lack of pollination or fertilization. The abortive pistillate flowers are often readily observed attached to or just below the cupule of a fully formed nut.

Cymule characteristics of Lithocarpus.

SUBGENUS species	Pistillate cymules		Staminate cymules	
	No. of flowers	No. of evident bracteoles	No. of flowers	No. of bracteoles
CYCLOBALANUS A. Camus				
aggregata Barnett	3	5+	3	5
bullata Hatusima ex Soep.	1	3	3	3
clementiana A. Camus	1,3	3	1,3	3
conferta Soep.	1	3	1	3
conocarpa Rehder	1	1	-	-
cyclophora A. Camus	-	-	3	5
daphnoidea A. Camus	1	3+	-	-
eichleri A. Camus	1	3+	-	-
encleisacarpa A. Camus	1	3	3	5
ewyckii Rehder	1	3	1,3	3
korthalsii (Endl.) Soep.	3	5+	3	5+
lampadaria A. Camus	5-7	7	5	7
lucida Rehder	1-3	1	3	3
lutea Soep.	1	3+	3	3
macphailii A. Camus	1-3	5+	3	5
mariae Soep.	1	3+	1	3
meijeri Soep.	1	1,3	1,3	3,5
neorobinsonii A. Camus	1	3	1	3
nieuwenhuisii A. Camus	1	3	-	-
pattaniensis Barnett	1-3	5-7	1	3-7
philippinensis A. Camus	-	-	1,3	1,3
rassa (Miq.) Rehder	1	3	1	3
reinwardtii A. Camus	1,3	3,5	1,3	3
sericobalanus Warb.	1	3	-	-
suffruticosa (Ridley) Soep.	1	3	3	3
GYMNOBALANUS A. Camus				
havilandii Barnett	1	3	1	3
kingiana A. Camus	1	3	1	3
konishii Rehder	1	3	3	5
lauterbachii Markgraf	1	3	1	3
LIEBMANNIA A. Camus				
hendersoniana A. Camus	3-5	5+	3-5	5+
LITHOCARPUS Markgraf				
beccariana A. Camus	1	1	1	1
maingayi Rehder	-	-	3	-
perakensis Soep.	1	3	-	-
turbinata (Stapf) Forman	1	3	1	3
PACHYBALANUS A. Camus				
amygdalifolia Hayata	1-3	3-7	3	5
nantoensis Hayata	1	1	1	5
truncata Rehder & Wilson	5	ca. 7	5	ca. 7
PASANIA A. Camus				
buddii (Merr.) A. Camus	3	3	3	3,7
caudatifolia Rehder	1	3	3+	3
celebica Rehder	1,3	3+	3	3
cooperta (Blanco) Rehder	1	3	1,3	3
curtisii (King ex Hooker f.) A. Camus	1	3	1	1
dasystachya (Miq.) Rehder	1,3	3,5	3	3
dealbata A. Camus	3,5	3+	3,5	9+
densiflora Rehder	1	1	3,5	5,7
edulis Nakai	1	-	1,3	1,3

Cymule characteristics of Lithocarpus (*continued*).

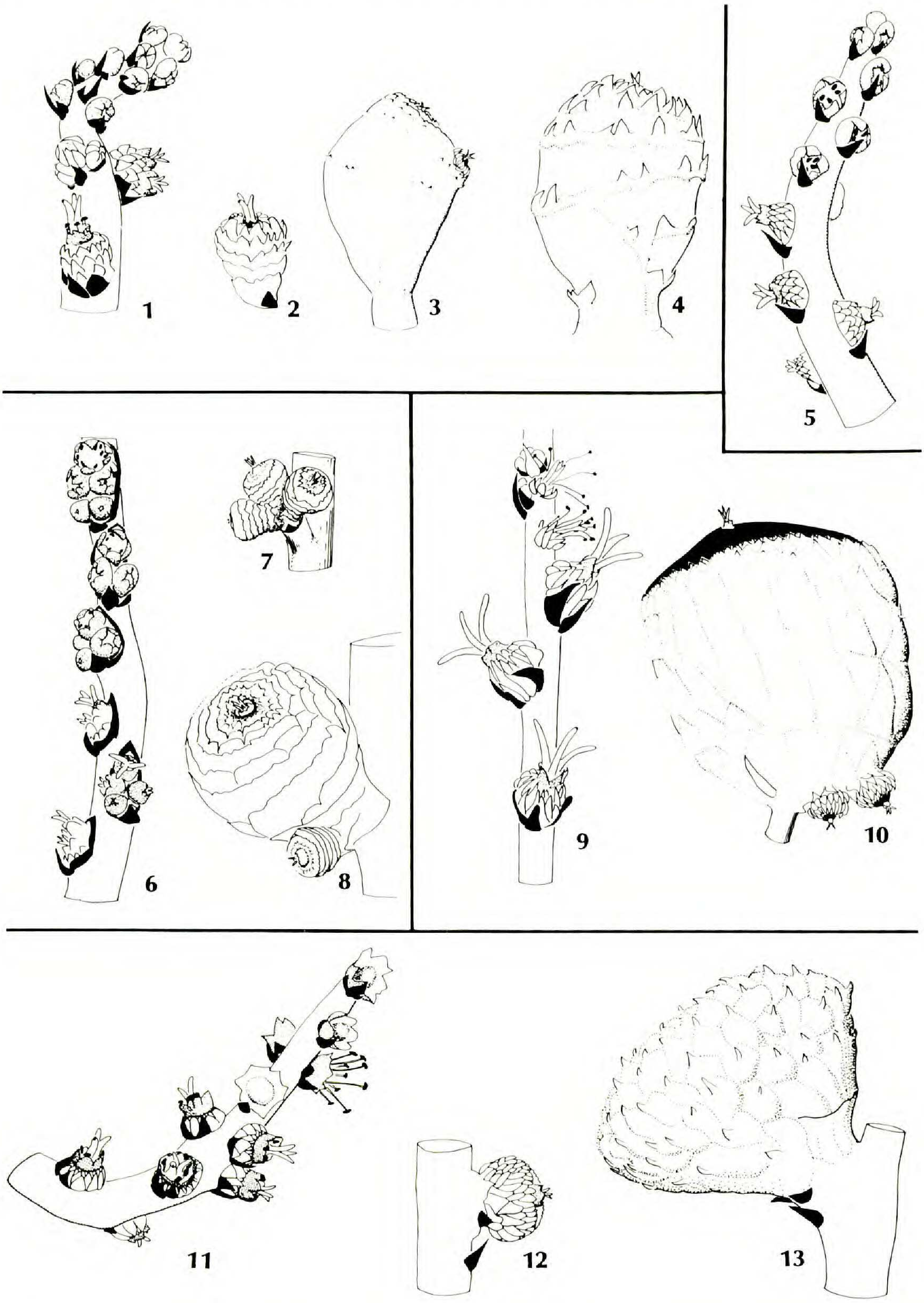
SUBGENUS species	Pistillate cymules		Staminate cymules	
	No. of flowers	No. of evident bracteoles	No. of flowers	No. of bracteoles
elegans (Blume) Hatusima ex Soep.	3-5	3	3-5	5+
elephantum A. Camus	1	3	1	3
falconeri Rehder	1	3	1	3
fenestrata Rehder	3	3	3	9+
formosana Hayata	3	3+	3	5
garrettiana A. Camus	3	3+	3	1
hancei Rehder	3	3+	3	3
harlandii Rehder	1,3	3	1,3	3,5
harmandii A. Camus	3-5	3?	4-7+	3
kawakamii Hayata	3-5	3+	-	-
papillifer Hatusima ex Soep.	1	1	2,3	-
polystachya Rehder	1-3	3+	3	3,5
rufovillosa Rehder	1	3	1,3	3
sabulicola A. Camus	1	3+	1	3
scortechinii A. Camus	1	3+	3	7+
soleriana Rehder	1	1	3	7+
sootepensis A. Camus	1,3	3	3	3
spicata Rehder & Wilson	3	3	3	5+
sundaica Rehder & Wilson	1	3+	1,3	1,3
ternaticupula Hayata	3	3+	3	3
thomsonii Rehder	3	3+	3	5
wallichiana Rehder	3	3	3	3
wrayi A. Camus	1	3+	3	3
PSEUDOCASTANOPSIS Hickel & A. Camus				
fissa A. Camus	1	1	1,3	4
SYNAEDRYS A. Camus				
cornea Rehder	1	3	3	3
kodaihoensis Hayata	1	3	1	3
pulchra Markgraf	1	3	1	3

In multi-flowered cymules the sequence of anthesis begins with the central (uppermost) flower and progresses to the subjacent pair and then to the lowest pairs (see, for example, FIGURES 29, 30). In three-flowered cymules the central (upper) flower opens first and the subjacent pair soon afterward.

The bracteoles that subtend the cymules vary within subgenera and species and sometimes between staminate and pistillate cymules in the same inflorescence (see TABLE). The number of bracteoles sometimes equals but more often exceeds the number of flowers in the cymule, but it is rarely less (see TABLE).

In both pistillate and staminate cymules there is a single, usually larger, primary bracteole centered below the cymule (see, for example, FIGURES 16, 17). Subsequent bracteoles are often smaller, sometimes progressively so, and are usually paired across the cymule.

The subtending bracteoles of the pistillate cymules sometimes grade into the cupular bracteoles (hereinafter called "scales"), but for the most part they are



FIGURES 1–13. 1–4, *Lithocarpus turbinata:* 1, spike tip at anthesis, staminate cymules above, pistillate and perfect below (bracteoles in black and perianth stippled in most figures); 2, pistillate flower in cupule at anthesis; 3, mature cupule with adventitious, abortive flower; 4, immature cupule. 5, *L. beccariana:* spike tip at anthesis, staminate (upper) and pistillate (lower) cymules with 1 flower. 6–8, *L. hendersoniana:* 6, spike tip at anthesis, staminate (upper) and pistillate (lower) cymules with 3 to 5 flowers; 7, pistillate cymule after anthesis, somewhat raised upon peduncle; 8, immature cupules, 1 abortive.

distinguished by their size (as the illustrations show), their greater thickness, and occasionally their coloration. In some cases the uppermost bracteoles are connate and form an entire or serrate border above the pistillate cymule, but usually all the bracteoles are free. While some of the bracteoles are deciduous or break off as the cupule expands after fertilization, the primary, and often other, bracteoles persist below the matured cupule. At least the primary bracteole is usually readily apparent at cupular maturity, although it is often greatly exceeded by the cupule and its scales.

The bracteoles of the staminate cymules are more easily seen because they are not crowded by cupular scales. They are more often connate than are those of the pistillate cymules, even within a species, and sometimes the connation is so extreme that an accurate count is impossible (see, for example, FIGURES 89, 94). In rare instances the partially connate upper bracteoles enclose smaller bracteoles that suggest a rudimentary cupule enclosing the staminate flowers (see FIGURE 62, uppermost cymule).

In staminate and pistillate cymules that have more than four bracteoles, it is usually possible to enumerate the bracteoles and bracteole pairs at least to the quaternary level or, if there is no connation, beyond. In many pistillate cymules, however, the intergradation of subtending cymule bracteoles with the cupular scales often makes such distinctions arbitrary beyond the primary or secondary bracteoles. Even in the earliest developmental stages of a few species that have been studied, it is not always possible to distinguish the first cupular scales from the subtending bracteoles.

PISTILLATE CYMULE ORGANIZATION AND CUPULAR STRUCTURE

Among and within subgenera, there are great differences in the relative contributions of the cupular scales to the mature cupules, which vary more than those of *Quercus*. The flowers, cymules, and immature and mature cupules are shown in FIGURES 1–111 for 38 species from seven subgenera. Camus (1948), in Volume 3 of her *Atlas*, illustrated many species but did not include details of cymule bracteoles or cupule development. Her plates are cited below to complement my illustrations.

SUBGENUS LITHOCARPUS. In both species that were studied developmentally (*Lithocarpus beccariana, L. turbinata*), the fruits are large, elongate, and figlike; the cupule encloses the nut almost entirely (FIGURE 4; Camus, 1948, *pl. 355*). In *L. turbinata* there are three obvious cymule bracteoles, above which the cupular scales are prominent at anthesis (FIGURE 1). These scales are pushed upward as the cupular lamellae extend, and some of the lamellae become excentric and disrupted in the process (FIGURES 2–4); the scales become widely

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9, 10, *L. cornea:* 9, upper portion of spike at anthesis, showing staminate and pistillate, 1-flowered cymules; 10, mature cupule with 2 abortive cupules fused to it. 11–13, *L. pulchra:* 11, spike tip at anthesis, showing staminate and perfect flowers; 12, lateral view of pistillate cymule some time after anthesis, showing 2 of 3 bracteoles; 13, immature cupule, showing scale-bearing tubercles and all 3 bracteoles. Figures 1, 2, 4, 10, 13, × 2; Figure 3, × 0.3; Figures 5–9, 11, 12, × 4.

separated, but many of them persist on the mature cupule (FIGURE 3). At maturity the primary bracteole also usually persists, but the secondary bracteoles do not; however, some scales remain near the base of the cupule. *Lithocarpus beccariana* has but one bracteole below each pistillate cymule, and above it are the cupular scales (FIGURE 5). At maturity the cupule is virtually scaleless, and the scale-bearing lamellae are greatly extended (Camus, 1948, *pl. 355*). FIGURE 3 shows an apparently adventitious, abortive flower and cupule borne well up on the mature, nut-enclosing cupule.

SUBGENUS LIEBMANNIA. The three-or-more-flowered pistillate cymules of *Lithocarpus hendersoniana* have an obvious primary bracteole below them, and a low ring of overlapping bracteoles above that forms a pointed cowl at the distal end of the cymule (FIGURE 6). After pollination the cymule becomes pedunculate, and the primary bracteole is elevated on the peduncle (FIGURE 7). The cupular lamellae are continuous at first but later become interrupted (FIGURE 8), perhaps because of the rupturing stresses of diametric growth. The mature nut is included in the cupule.

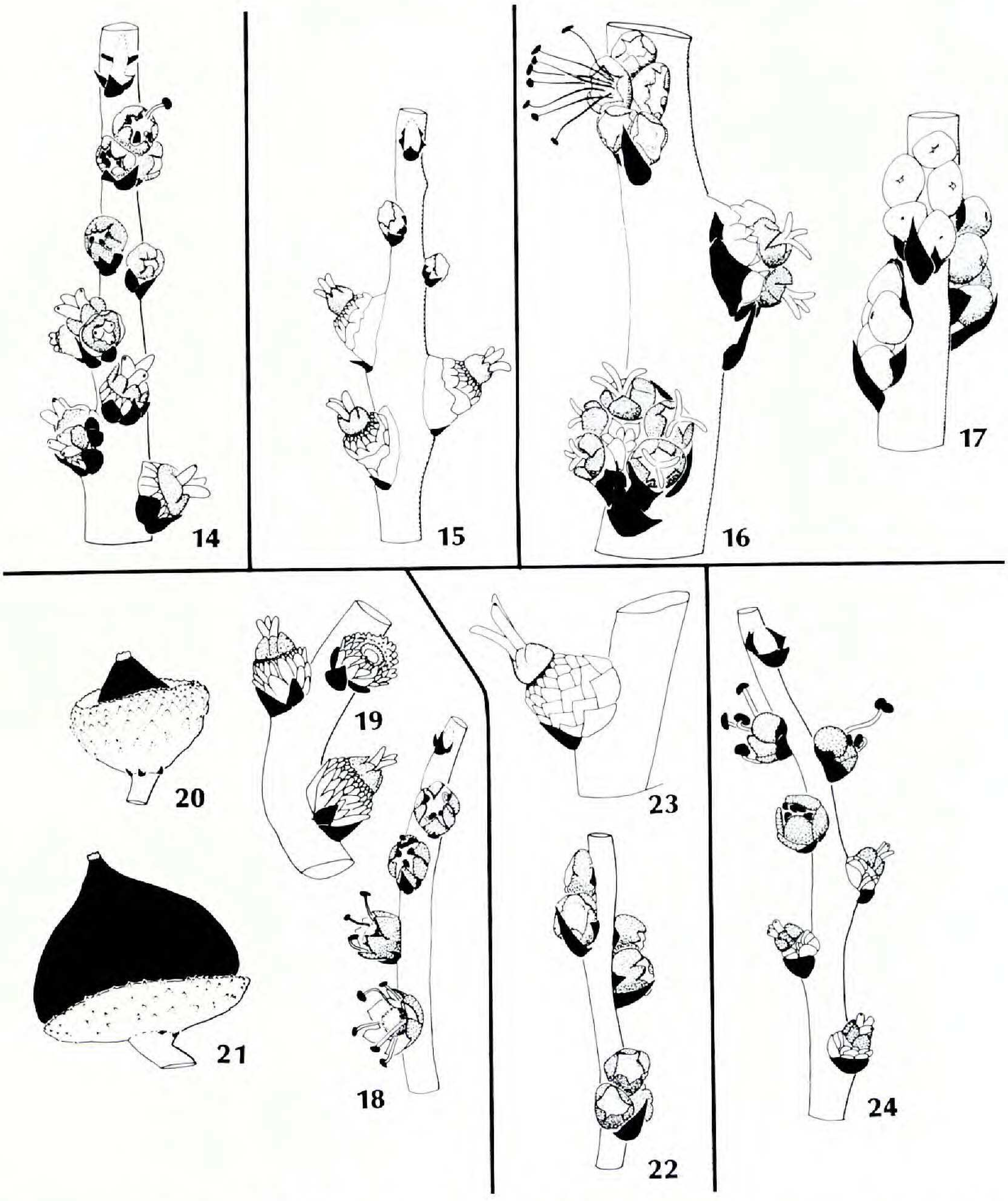
SUBGENUS SYNAEDRYS. The cupular scales of *Lithocarpus cornea* are prominent at anthesis, and the three subtending bracteoles are clearly distinguished (FIGURE 9). Enormous expansion of the cupular lamellae is accompanied by great growth in the scales, which become appressed and fused to the lamellae (FIGURE 10). The mature cupule covers most of the nut, except for a broad polar area. FIGURE 10 shows two abortive flowers and cupules attached at the base of the cupule.

In *Lithocarpus pulchra* the three bracteoles of the one-flowered cymule are evident at anthesis (FIGURES 11, 12) and in fruit (FIGURE 13), but an additional ring of bracteoles that surrounds the cupular scales quickly loses its identity as the cupule enlarges. The scales of the mature cupule are widely separated, each of them raised upon a mound of cupular tissue (FIGURE 13; Camus, 1948, *pl. 370*).

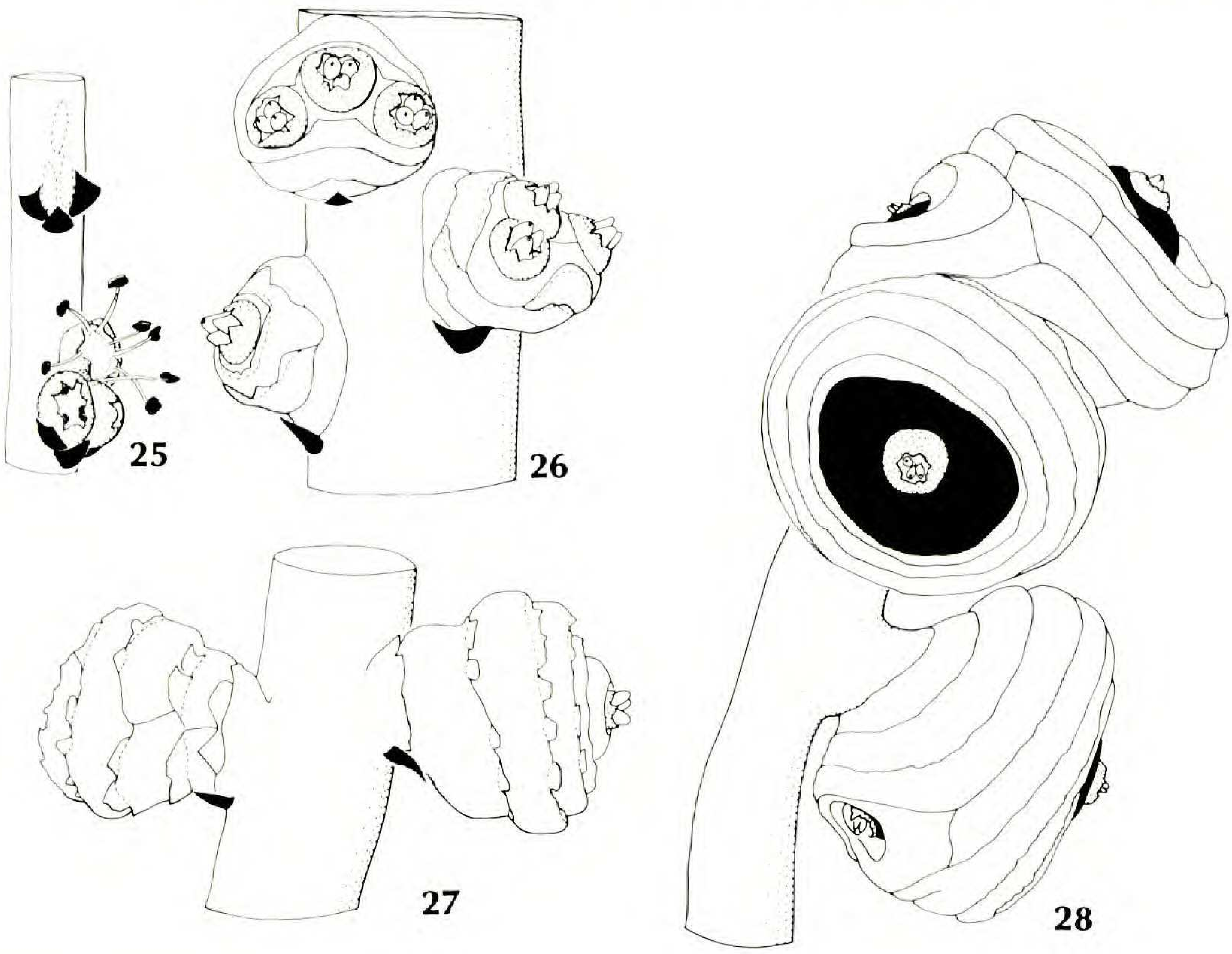
SUBGENUS PACHYBALANUS. In both *Lithocarpus amygdalifolia* and *L. truncata* at least seven bracteoles subtend the multi-flowered cymules (FIGURES 14, 16); in the former species the one-flowered cymules have but three (FIGURE 14). There are other bracteoles within the multi-flowered cymules. The cupular scales are hidden at anthesis by all these bracteoles, but they quickly become evident afterward. The mature cupule encloses much of the nut and is adorned with large, widely spaced cupular scales (Camus, 1948, *pl. 377*). The cymules of *L. nantoensis* have just one bracteole, the primary, and above it is a ring of presumably fused bracteoles that entirely encircles the cupule (FIGURE 15).

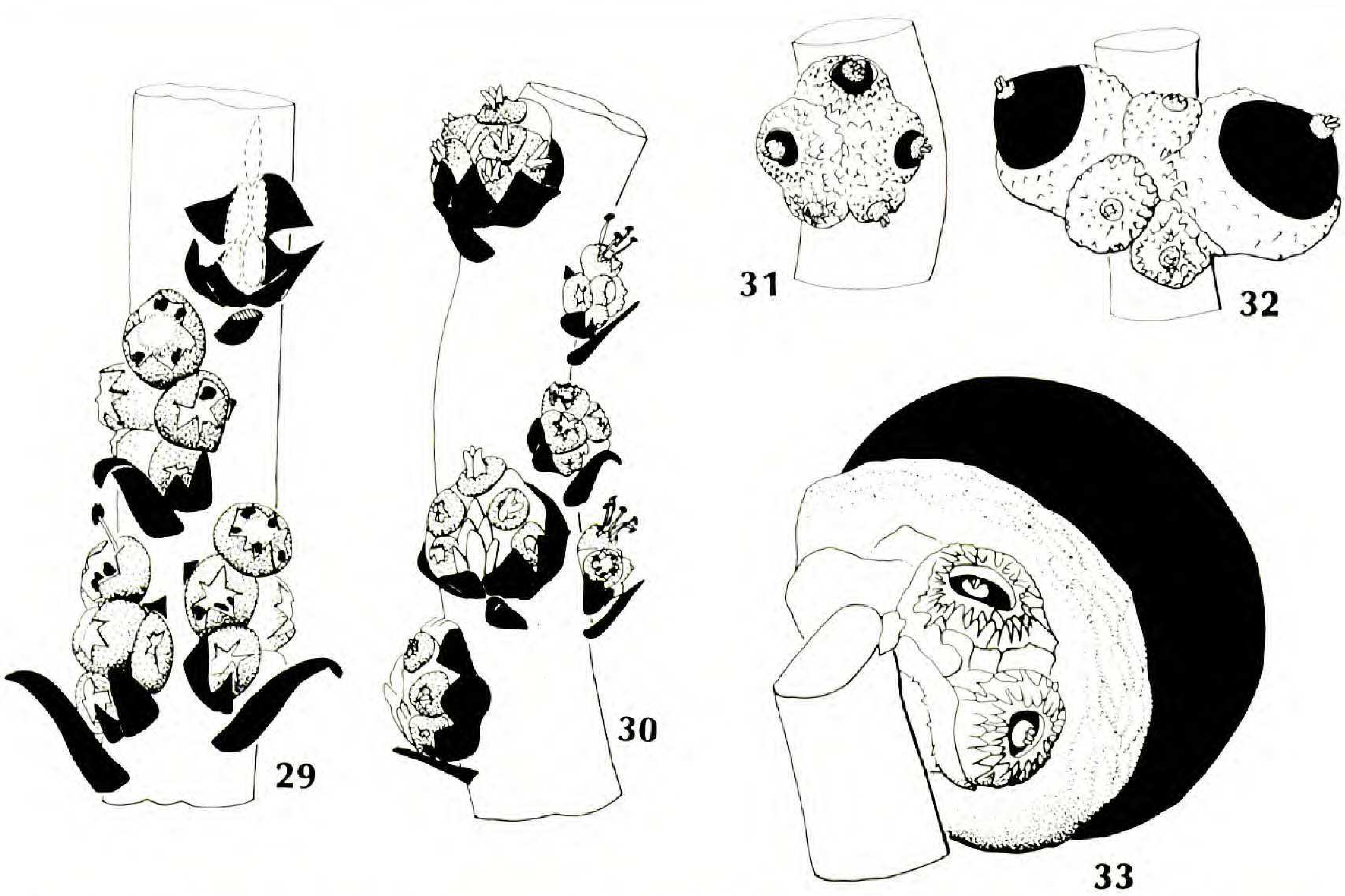
SUBGENUS GYMNOBALANUS. Three distinct bracteoles subtend each one-flowered cymule of *Lithocarpus havilandii* at anthesis (FIGURE 19), and they usually persist below the mature cupule (FIGURES 20, 21). The numerous cupular scales are prominent at anthesis (FIGURE 19) but are mostly adnate to the cupule at maturity (FIGURE 21), at which time they are not obviously arranged in concentric rings. The nut is enclosed by the cupule when immature but is mostly exposed at maturity (FIGURES 20, 21).

The one-flowered cymules of *Lithocarpus konishii* and *L. lauterbachii* have



FIGURES 14–24. 14, *Lithocarpus amygdalifolia:* spike tip at anthesis, staminate and pistillate cymules 1- to 3-flowered, flowers removed from uppermost staminate cymule to reveal 5 bracteoles. 15, *L. nantoensis:* spike tip at anthesis, staminate and pistillate cymules 1-flowered, uppermost staminate cymule with flower removed to reveal 5 bracteoles. 16, 17, *L. truncata:* 16, portion of spike at anthesis with 1 staminate and 2 pistillate cymules, all 5-flowered; 17, portion of staminate spike, showing 5-flowered staminate cymules with bracteoles and unopened flowers. 18–21, *L. havilandii:* 18, 19, segments of staminate and pistillate spikes at anthesis, all cymules 1-flowered; 20, 21, immature and mature fruits, showing persistent bracteoles below cupule. 22, 23, *L. konishii:* portions of staminate and pistillate spikes, showing 3-flowered staminate and 1-flowered pistillate cymules. 24, *L. lauterbachii:* near-terminal segment of spike at anthesis, all cymules 1-flowered. Figures 14, 20, 21, × 2; all others, × 4.





FIGURES 25–33. 25–28, *Lithocarpus lucida:* 25, segment of staminate spike with 2 3-flowered cymules, upper 1 with flowers removed to reveal 3 bracteoles; 26, segment of pistillate spike with 1 1-flowered and 2 3-flowered cymules after anthesis; 27, 2 1-flowered cymules with immature fruits, cupular scales evident; 28, immature fruits, older than those of Figure 27, cupular lamellae now devoid of scales, abortive fruit visible at lower end of lower cupule. 29–33, *L. lampadaria:* 29, segment of staminate spike,

a primary bracteole and, above it, a ring of free but overlapping bracteoles around the cupule (FIGURES 23, 24). In both species the mature cupule covers less than half of the broad, low nut, and it is heavily invested with overlapping cupular scales (Camus, 1948, *pl. 385*).

SUBGENUS CYCLOBALANUS. The mature cupule is often devoid of cupular scales (FIGURES 28, 33, 35, 41, 44, 55–57, 66), or it may have weakly developed scales that are widely separated (FIGURES 47, 51). In all the species of this subgenus illustrated, the early developmental stages clearly show the presence of cupular scales (FIGURES 27, 31, 32, 34, 38, 42, 43, 45, 46, 49, 50, 52, 59, 65). Many scales are deciduous or become distorted and exceeded by the massive growth of the cupule, and the mature cupule is then naked or nearly so. The cupular lamellae are more or less concentric in many species, but in a few they are not distinguishable at maturity (FIGURES 33, 35). In these the mature cupule consists of random or vaguely concentric scaleless enations. In some multi-flowered cymules the lowest few lamellae embrace all the flowers (FIGURES 26, 33, 39), but each flower eventually develops its own cupule (FIGURES 28, 33, 39). Other multi-flowered cymules lack such collectively embracing lamellae, and the flower cupules are distinct from the earliest stages (FIGURES 49, 50, 64).

The pistillate cymules of *Lithocarpus lucida* (FIGURES 26–28) are one- or three-flowered. All three flowers do not ordinarily mature in the latter case (FIGURE 28), nor do some of the one-flowered cymules. There is but one discernible subtending bracteole below each cymule, whether it is one- or three-flowered. Above it is a ring of tissue that perhaps represents fused bracteoles and that forms the first lamella of the cupule embracing all the flowers. The next structures to appear are partial lamellae that collectively embrace all the flowers (FIGURES 26, 27). It is not until well after pollination that the truly concentric, cupular lamellae arise in acropetal sequence. The scales are readily visible at these early stages. As the cupules near maturity, the scales have fallen or have become split and stretched beyond recognition; the cupule then appears to be scaleless (FIGURE 28). The massive growth of the cupular lamellae causes distortions among the contiguous cupules so that at least the first-formed (lowest) lamellae are often distinctly excentric. Abortive flowers become partially or completely buried in the maturing cupule (e.g., the central flower in the upper cymule and the lateral flowers in the lower cymule of FIGURE 28). At maturity the cupule covers less than half of the nut (Camus, 1948, *pl. 386*).

In *Lithocarpus reinwardtii* the cymules are also one- or three-flowered (FIGURES 37–40). The one-flowered cymules are subtended by three distinct bracteoles, above which the scale-bearing concentric lamellae appear in acropetal sequence. The last few lamellae to form are weakly developed and show no external evidence of scales (FIGURES 40, 41). The mature cupule is scaleless, although

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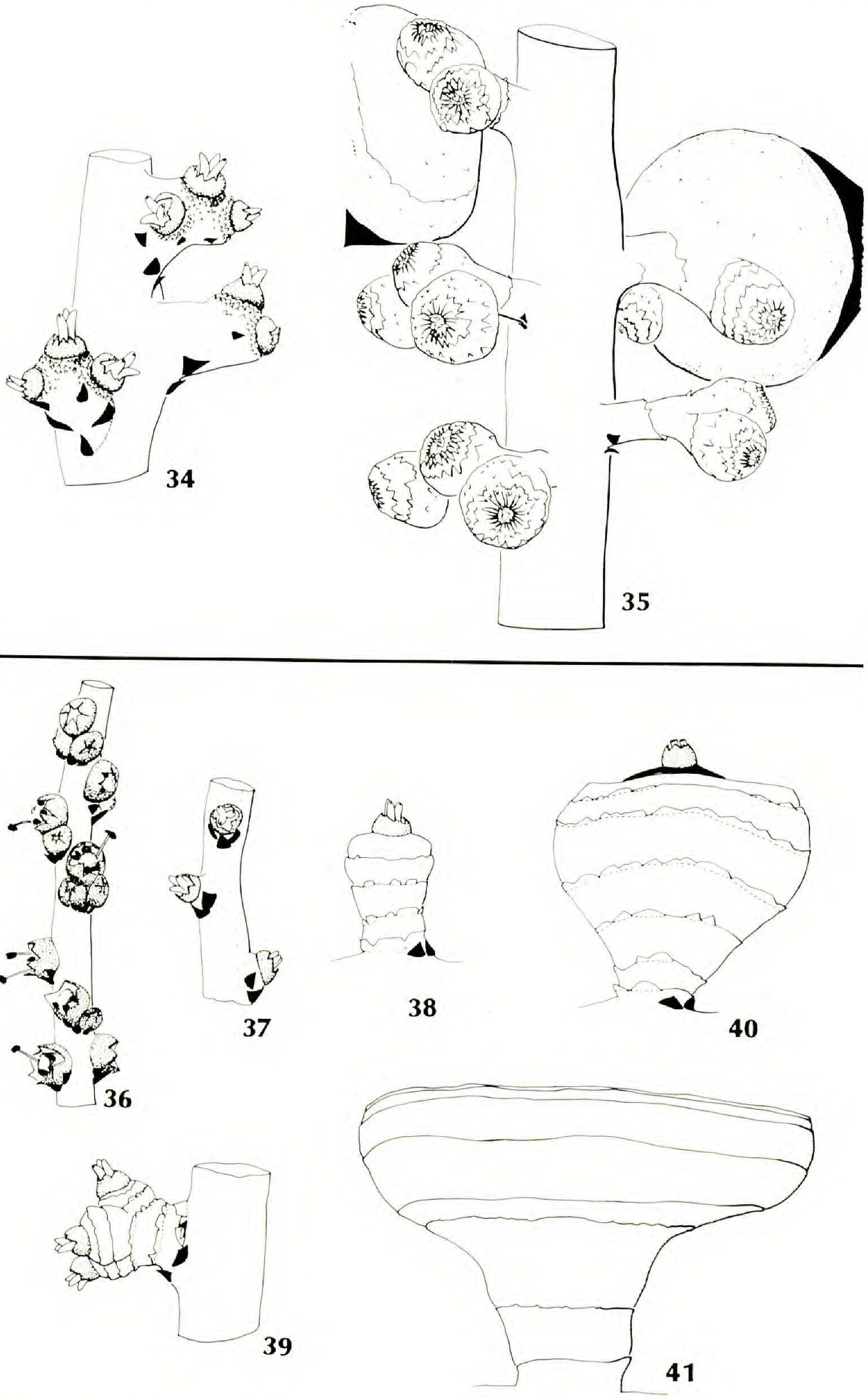
showing 5-flowered cymules, upper 1 with flowers removed to reveal 7 bracteoles; 30, segment of spike showing mixture of staminate and pistillate cymules, all multi-flowered; 31, 32, maturing pistillate cymules after anthesis, some flowers and their cupules abortive; 33, mature fruit with 2 basal, abortive flowers in cupules. Figures 28, 33, × 2; all others, × 4.



FIGURES 34–41. 34, 35, *Lithocarpus aggregata:* 34, segment of pistillate spike at anthesis, showing pedunculate 3-flowered cymules and their bracteoles; 35, segment of pistillate spike bearing mature fruits and abortive cupules. 36–41, *L. reinwardtii:* 36, segment of staminate spike at anthesis, showing 1- and 3-flowered cymules; 37, 1-flowered pistillate cymules at anthesis; 38–40, maturing cupules with evident scales; 41, mature cupule (nut removed), showing essentially scaleless lamellae. Figure 41, × 2; all others, × 4.

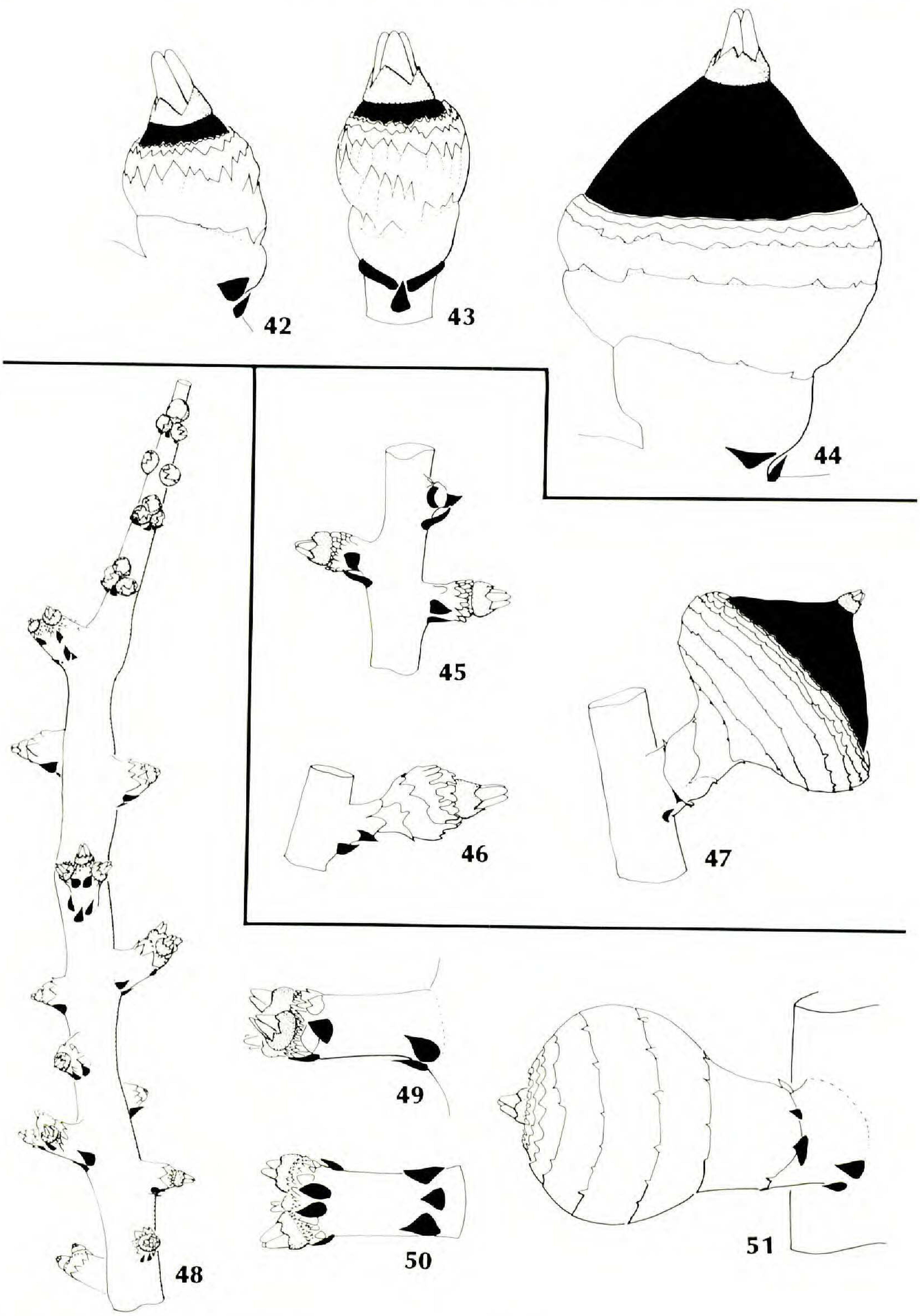
some evidence of scales can be seen in the lowest few lamellae (FIGURE 41). The three-flowered cymules, which are less common in my specimens than the one-flowered, are subtended by at least five distinct bracteoles (FIGURE 39), and there are other structures at the base of the cymule that may also represent subtending bracteoles. The first two lamellae to form surround all three flowers, but later lamellae embrace only one. Further details are shown by Camus (1948, *pl. 397*).

The one-flowered cymules of *Lithocarpus bullata* and *L. ewyckii* are also subtended by three obvious, distinct bracteoles (FIGURES 42–47) that persist below the mature cupule. The first lamella to form above the bracteoles of *L. bullata* bears a few scales (FIGURES 42, 43) that persist to maturity of the cupule. Succeeding lamellae have more scales, many of which persist but become widely separated as the diameter of the cupule increases (FIGURE 44). The uppermost lamellae are scaleless from their earliest stages. The first lamellae of *L. ewyckii* are more irregular than those of *L. bullata,* but they, too, are scaly. The later lamellae are regular and concentric and retain many of their scales into maturity, at which time the scales are widely spaced, sometimes reflexed, and often broken (FIGURE 47).

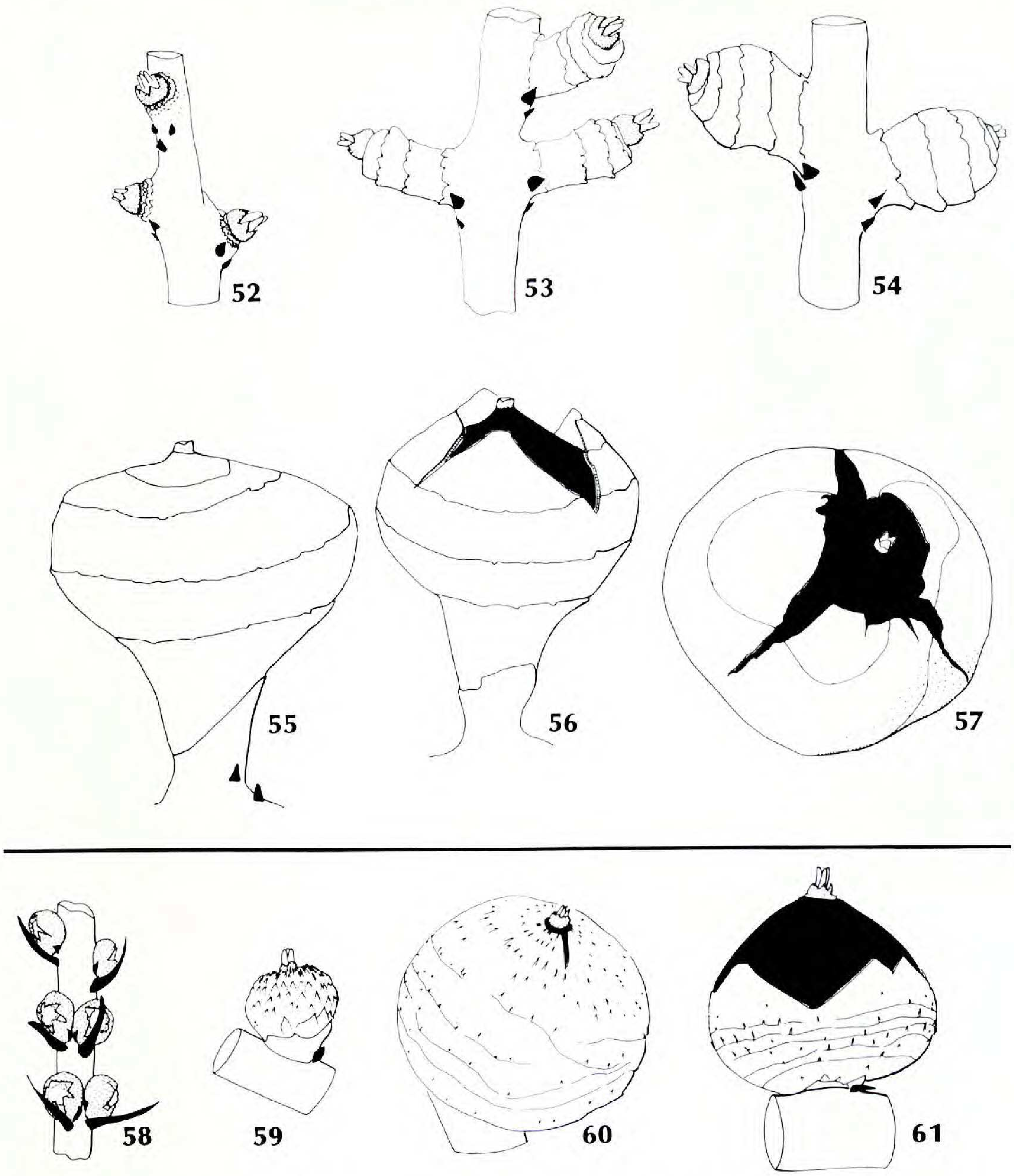
The cymules of *Lithocarpus macphailii* are distinctly pedunculate at anthesis (FIGURES 49, 50), but the peduncle does not lengthen very much as the cupule matures. There are three basal bracteoles (shown in lateral and ventral views in FIGURES 49 and 50, respectively). Another series of distinct bracteoles is evident at the distal end of the peduncle, just below the individual flowers (these are shown in black for emphasis in FIGURES 48–51). These, too, persist into maturity of the cupule (FIGURE 51), and they are readily distinguished by their location, thickness, and color from the other bracteoles below the flowers. Each flower develops its own cupule, but there is a loose ring of distinct or partially fused bracteoles that embraces all the flowers below their cupules (FIGURES 49, 50). As the cupular lamellae expand, the scales become widely separated but (as in the other species of this and many other subgenera) do not enlarge (FIGURE 51). At full maturity, only a small upper portion of the nut is visible (Camus, 1948, *pl. 407*).

Most of the cymules of *Lithocarpus encleisacarpa* are one-flowered, and each is subtended by three bracteoles (FIGURES 52–55). At anthesis the cymules are sessile, but they become pedunculate by elongation of the first few lamellae of the cupule (FIGURES 52–56); succeeding lamellae increase in diameter more than in length, and the mature cupule is turbinate. The cupular scales are evident at anthesis (FIGURE 52) but are barely apparent when the cupule matures (FIGURES 55–57). As the nut enlarges, the cupule ruptures, usually along three irregular arcs that cut through some of the upper lamellae (FIGURES 56, 57; Camus, 1948, *pl. 406*).

The pistillate cymules of *Lithocarpus neorobinsonii* have one primary bracteole at the base (FIGURES 59, 61); above this is an irregular lamella that may represent other, fused bracteoles. The somewhat irregular lamellae (even the uppermost, poorly developed ones) of the cupule retain their scales to maturity. The upper part of the cupule ruptures irregularly as the nut enlarges, with the tears extending only into the region of weak development of the lamellae (FIGURES 60, 61; Camus, 1948, *pl. 410*).

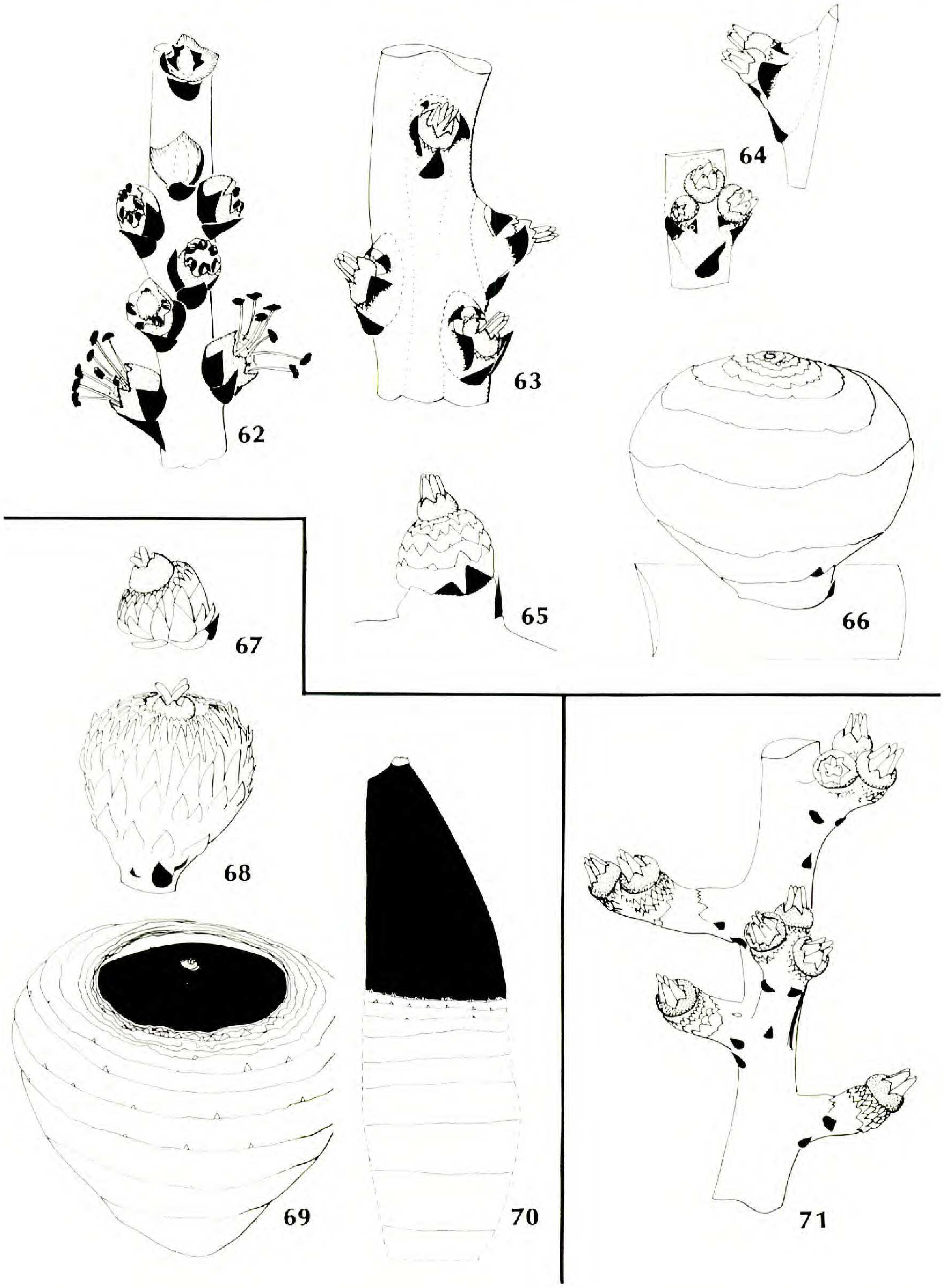


FIGURES 42–51. 42–44, *Lithocarpus bullata:* 42, 43, lateral and basal views of 1-flowered pistillate cymule somewhat beyond anthesis, showing bracteoles and young cupule; 44, nearly mature fruit, showing bracteoles and cupular scales during cupular enlargement. 45–47, *L. ewyckii:* 45, segment of pistillate spike at anthesis, showing 1-flowered cymules and their 3 bracteoles; 46, pistillate cymule somewhat after anthesis, showing early, scaly stages of cupular lamellae; 47, nearly mature fruit, showing retained bracteoles and cupular lamellae with their remote scales. 48–51, *L. macphailii:* 48, spike tip at anthesis with 1- and 3-flowered cymules, staminate above and pistillate below; 49, 50, pistillate,



FIGURES 52–61. 52–57, *Lithocarpus encleisacarpa:* 52–54, 1-flowered pistillate cymules at anthesis and in early fruit, 3 bracteoles evident below each cymule, cupular scales evident at anthesis (FIGURE 52) but becoming remote and ruptured as cupule matures; 55, mature cupule with nearly scaleless lamellae; 56, 57, dehiscing cupule in lateral and polar views. 58–61, *L. neorobinsonii:* 58, segment of staminate spike at anthesis, cymules 1-flowered and with 3 bracteoles; 59, pistillate, 1-flowered cymule after anthesis, cupular scales evident; 60, nearly mature cupule with scales now remote and lamellae weakly developed; 61, mature cupule, upper portion dehisced irregularly and revealing nut. Figures 52–54, 58, × 4; all others, × 6.

3-flowered cymules at anthesis, lateral and basal views (cymules pedunculate from anthesis); 51, nearly mature cupule with persistent bracteoles and remote cupular scales. Figures 47, 51, × 2; all others, × 4.



FIGURES 62–71. 62–66, *Lithocarpus pattaniensis:* 62, segment of staminate spike, showing 1-flowered cymules, each with 3 or more bracteoles, upper 2 cymules with flower removed, uppermost cymule showing presence of inner set of bracteoles; 63, 64, 1- and 3-flowered pistillate cymules at anthesis; 65, 1-flowered pistillate cymule some time after anthesis, showing beginnings of lamellar growth of cupule, scales evident; 66, nearly mature cupule with lamellae prominent, scales now remote and ruptured, bracteoles evident. 67–70, *L. rufovillosa:* 67–69, maturing 1-flowered pistillate cymule with 3 bracteoles, scales prominent near anthesis (FIGURE 67) but lamellae prominent in fruit (FIGURES

Above the obvious primary bracteole of the one- and three-flowered cymules of *Lithocarpus pattaniensis* are other, basally fused bracteoles that encircle the flower(s) (FIGURES 63–65). There are usually four of these in the one-flowered cymules but more in the three-flowered ones. Some of these bracteoles persist into maturity of the cupule (FIGURE 66). The cupular scales are evident at anthesis (FIGURES 63, 64) but are tiny and often ruptured on the massive lamellae of the mature cupule (FIGURE 66). The scales are adjacent at anthesis but become separated during cupular expansion (FIGURES 65, 66). When the cupule is fully mature, it reveals a small portion of the nut (Camus, 1948, *pl. 517*).

The mature cupule of *Lithocarpus aggregata* does not show the obvious lamellae of the above-described species. Instead, it bears vaguely defined rows of enations that carry little or no evidence of cupular scales (FIGURE 35). However, cupular scales and lamellae are clearly evident in earlier developmental stages (FIGURES 34, 35). At anthesis the three-flowered cymules are pedunculate, and the peduncle is evident through maturity of the fruit (FIGURE 35). There are three bracteoles under each cymule, and above them are two more, each near a lateral flower; there is no bracteole immediately below the central flower (FIGURE 34). These persist into fruit. There is one lamella (or sometimes two) encircling the peduncle, but above it the lamellae embrace single flowers (FIGURE 35). After several obvious lamellae have formed, the succeeding ones are, from their inception, indistinct; it is they that form the irregular rows of enations in the upper part of the cupule.

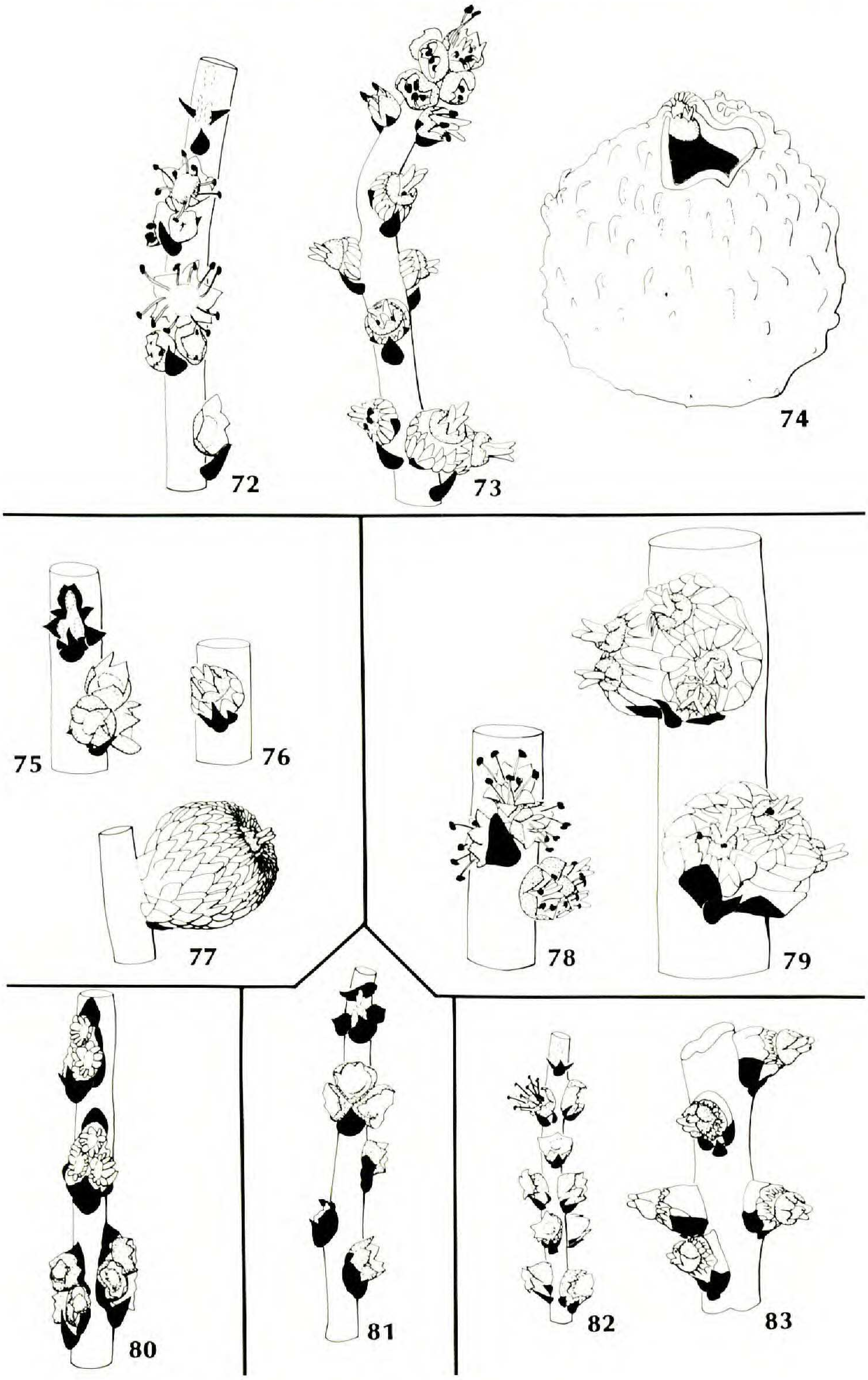
The pistillate cymules of *Lithocarpus lampadaria* often have five flowers, but more or fewer are common. Below each cymule is a single, distinct primary bracteole, above which is a series of six or so free but overlapping paired bracteoles (FIGURE 30). The primary bracteole and some of the others persist into fruit, but they are often completely distorted by the massive growth of the cupules and the resulting juxtaposition of the abortive flowers (FIGURES 32, 33). Of the hundreds of fruiting cymules examined, none bore more than three fully developed nuts, and most had none, one, or two.

SUBGENUS PASANIA. The cymule bracteole patterns of this subgenus resemble those of the other subgenera, but the cupular ornamentation is very diverse.

There are three bracteoles subtending the one-flowered pistillate cymule of *Lithocarpus rufovillosa* (FIGURE 68), and they persist into fruit. The cupular scales are evident at anthesis (FIGURE 67), and soon thereafter their alignment in rows is apparent (FIGURE 68). The massive growth of the lamellae separates the scales, many of which fall, leaving the cupule barely scaly at maturity (FIGURES 69, 70). In fact, many of the lower lamellae are scaleless (FIGURES 69, 70).

The distinctively pedunculate one- and three-flowered cymules of *Lithocar-*

69, 70); 70, segment of mature fruit, cupule covering about half of nut, scales retained only on upper lamellae. 71, *L. sootepensis:* segment of pistillate spike very soon after anthesis, cymules 1- and 3-flowered and with 3 bracteoles, peduncle evident at anthesis and eventually carrying mature fruits. Figures 66, 70, × 2; all others, × 4.



FIGURES 72–83. 72–74, *Lithocarpus wrayi:* 72, segment of staminate spike at anthesis, showing 1- and 3-flowered cymules, uppermost 1 with flowers removed to reveal 3 bracteoles; 73, spike tip with distal, 1-flowered staminate cymules and 1- and 2-flowered pistillate cymules, all with 3 bracteoles; 74, nearly mature cupule, scales basally adnate, upper portion broken away to reveal nut within. 75–77, *L. scortechinii:* 75, segment of staminate spike with 3-flowered cymules, upper 1 with flowers removed to reveal complex bracteole pattern; 76, 1-flowered pistillate cymule at anthesis, 3 bracteoles shown; 77, pistillate cymule after anthesis, showing extensive growth of cupular scales. 78, 79, *L.*

pus sootepensis each have a basal primary bracteole and a pair of secondary bracteoles that become elevated on the elongating peduncle (FIGURE 71). The cupular scales are well developed soon after anthesis and are evident in the mature cupule (Camus, 1948, *pl. 416*).

Three bracteoles subtend the one- or several-flowered cymules of *Lithocarpus wrayi* (FIGURE 73), and at least the primary bracteole can be seen below the mature cupule. The scales of the cupule are large at anthesis, and they remain prominent on the cupule in fruit, eventually becoming reflexed (Camus, 1948, *pl. 441*). The cupule does not show lamellae, although the persisting, subulate scales are aligned in concentric rows (FIGURE 74).

A primary bracteole and a pair of secondary ones subtend the pistillate cymules of *Lithocarpus hancei* (FIGURE 84). Most of the cymules have three flowers, but some of the more distal ones are one-flowered (FIGURE 84). A ring of connate bracteoles surrounds the flowers, and within that (but not visible in FIGURE 84) are the young cupules. As the nut and cupule begin to grow, the cupular scales emerge (FIGURE 86, lower, abortive cymule); at maturity the relatively small cupule shows irregular rings of annular enations, most of which bear a tiny cupular scale (FIGURE 86, mature nut and cupule; Camus, 1948, *pl. 415*).

The numerous scales of *Lithocarpus papillifer* (FIGURE 87), so evident at anthesis, remain small and adpressed on the mature cupule. There is but one obvious bracteole below each one-flowered cymule.

The long cupular scales of *Lithocarpus garrettiana* are evident from anthesis onward (FIGURES 79, 90–92), elongating considerably during cupular growth so as to be trichomelike at maturity. In the lower part of the mature cupule, the scales are in concentric rows (FIGURE 92); those higher up are usually crowded, and their arrangement in rows is not evident. The drying, dehiscing cupule splits open along three radial arcs (FIGURE 91) that extend halfway or less down the cupule, the upper part of the cupule sometimes breaking away in a crudely circumscissile dehiscence (FIGURE 92). There is some variation in dehiscence pattern of the cupule; only the usual one is illustrated in FIGURES 91 and 92 (cf. Camus, 1948, *pl. 434*).

As in many species of subg. *Cyclobalanus*, the mature cupule of *Lithocarpus soleriana* has concentric lamellae bearing vestiges of cupular scales (FIGURE 96; Camus, 1948, *pl. 467*). The primary bracteole subtends the one-flowered cymule and is surmounted by a ring of partially connate bracteoles that enclose the cupule; the cupular scales are evident at anthesis (FIGURE 95). With ex-

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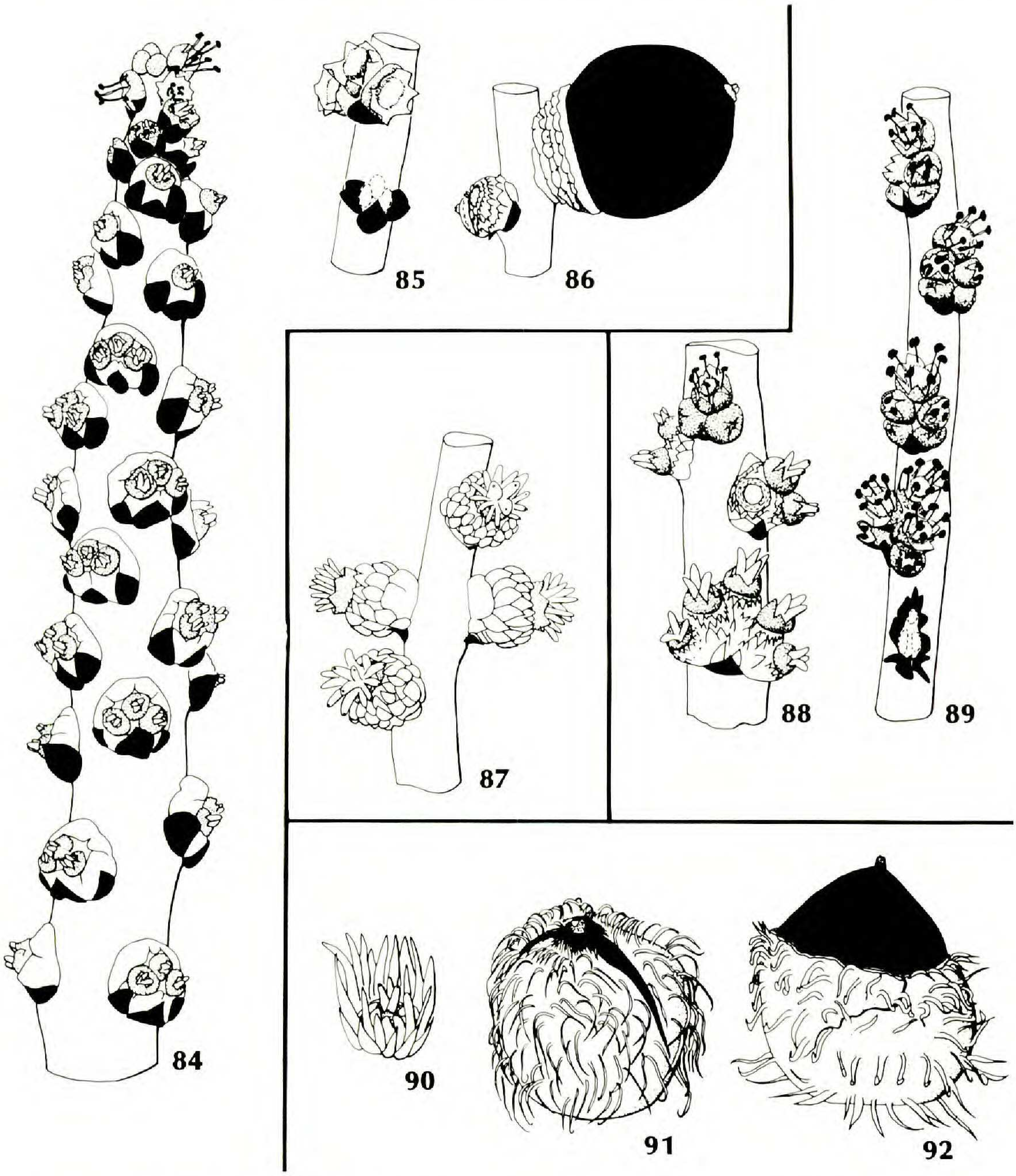
garrettiana: 78, segment of staminate spike, showing 3-flowered cymules with 1 bracteole; 79, segment of pistillate spike at anthesis, showing 3- and 4-flowered cymules, each subtended by 3 bracteoles. 80, *L. fenestrata:* segment of staminate spike in anthesis, showing 3-flowered cymules, upper 2 with flowers removed to reveal interior sets of bracteoles (not in black). 81, *L. harlandii:* segment of staminate spike at anthesis with 1- and 3-flowered cymules, uppermost 1 with flower removed to reveal bracteoles. 82, 83, *L. sabulicola:* 82, segment of staminate spike at anthesis, showing 1-flowered cymules, uppermost 1 with flower removed to reveal 3 bracteoles; 83, segment of pistillate spike at anthesis showing 1-flowered cymules with 3 bracteoles. Figures 74, 77, × 2; all others, × 4.



FIGURES 84–92. 84–86, *Lithocarpus hancei:* 84, spike tip at anthesis, showing few distal, staminate, 1-flowered cymules, each with 3 bracteoles, pistillate cymules 3-flowered and with 3 bracteoles; 85, segment of staminate spike with 3-flowered cymules, each with 3 bracteoles, lower cymule with flowers removed; 86, segment of fruit-bearing pistillate spike, 1 cymule with only abortive flowers and cupules, mature cupule with scale-bearing enations. 87, *L. papillifer:* segment of pistillate spike soon after anthesis, 1-flowered cymules each with 1 obvious bracteole, numerous styles on each flower. 88, 89, *L. dealbata:* 88, segment near tip of spike, with 1 3-flowered staminate cymule, pistillate cymules 3- and 5-flowered, each with 1 obvious bracteole; 89, segment of staminate spike at anthesis, most cymules 5-flowered, lowest 1 with 3 flowers removed to reveal complex bracteole pattern. 90–92, *L. garrettiana:* 90, flower in cupule soon after anthesis, cupular scales already very long; 91, mature cupule invested with elongate, recurved scales and showing 3 lines of dehiscence from upper pole; 92, mature cupule, dehisced upper portion fallen away. Figures 86, 91, 92, × 2; all others, × 12.

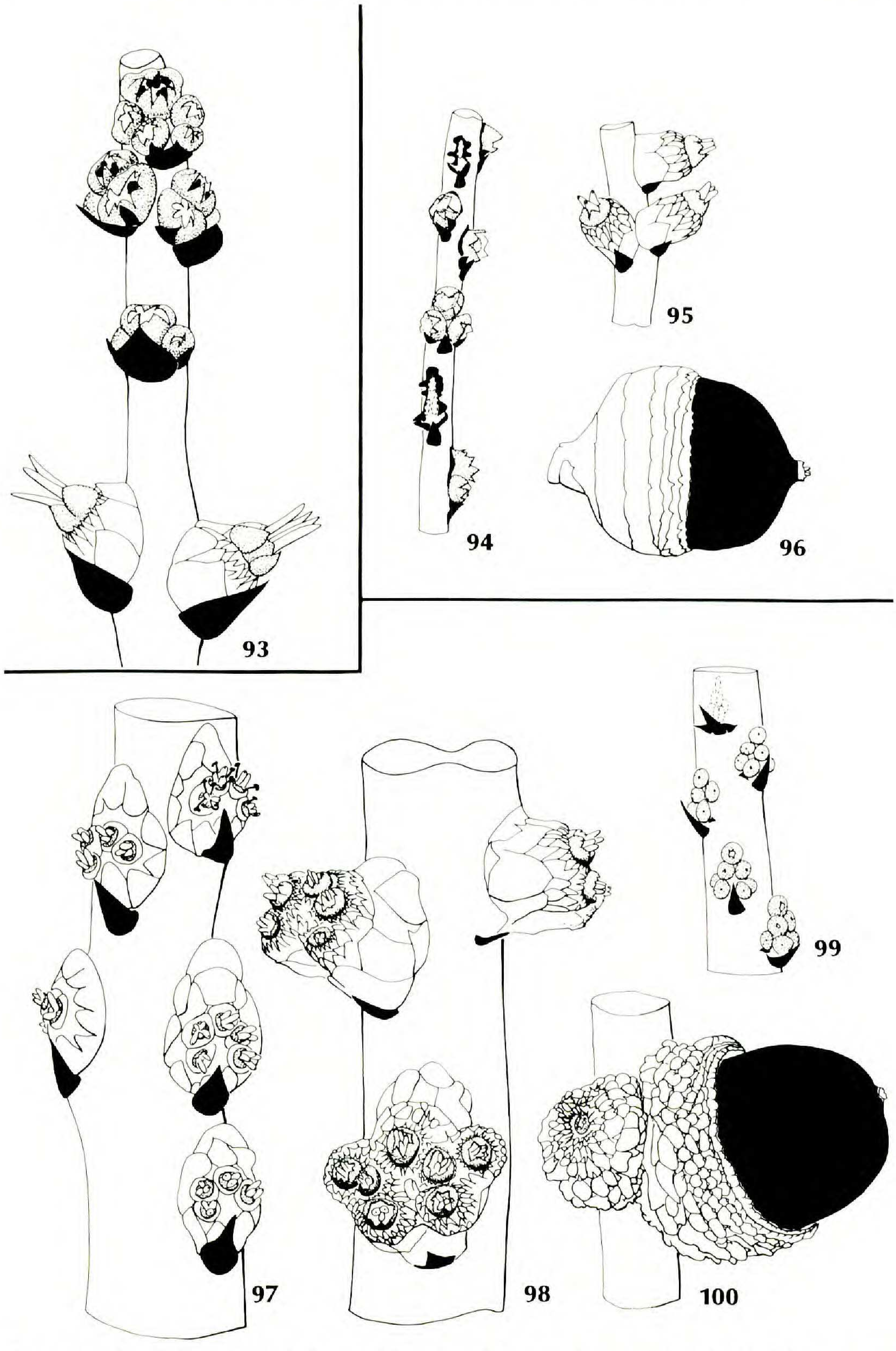
pansion of the cupule as maturity nears, the scales are separated and often ruptured, but most of them persist.

The pistillate cymules of *Lithocarpus harmandii* are among the most complex in the genus. They have one to seven flowers and are surrounded by a mass of bracteoles (FIGURES 97, 98). Below each cymule is a single obvious primary bracteole, above which is a complex ring of barely connate bracteoles. At anthesis the cupular scales are not evident because they are hidden by the ring of bracteoles (FIGURE 97), but soon thereafter they become prominent (FIGURE 98). Each flower develops its own cupule, but only one or two—very rarely three—mature into fruit. The abortive flowers continue to grow for some time and develop obvious but small cupules (FIGURE 100). The cupule surrounding a mature nut is a mass of more or less concentrically arranged enations, most of which bear a tiny cupular scale (FIGURE 100; Camus, 1948, *pls. 470, 471*).

The pistillate cymules of *Lithocarpus elegans* are also complex. They usually hold three to five flowers, with a few having one or six or more (FIGURE 101). A primary bracteole and a lateral pair of secondary ones are attached to the elevated buttress that bears the flowers (FIGURES 101, 103). There are no other obvious bracteoles in the cymule at anthesis, but there are faint ridges on the buttress that suggest a ring of reduced bracteoles (not visible in FIGURE 101). There are no readily discernible cupular scales at anthesis, but they appear soon thereafter. Their arrangement in concentric rows is then evident. The rings of scales are very tightly compressed, and the scales are appressed but readily visible in the mature cupule (FIGURE 103; Camus, 1948, *pl. 481*). As the nut matures, the partially enclosing cupule ruptures along four or five arcs (FIGURE 103).

One primary bracteole and a pair of lateral bracteoles, one below each lateral flower, are characteristic of the three-flowered cymules of *Lithocarpus wallichiana*. There is also a ring of partially connate bracteoles that partially surrounds the cymule (FIGURE 105). The cupular scales are not entirely concealed by these bracteoles at anthesis, and they later become prominent (FIGURE 106). Although it is not obvious in FIGURE 106, the scales are aligned in concentric rows. At maturity of the cupule, the scale-bearing concentric lamellae are evident; they have persistent, separated, torn scales (FIGURE 107; Camus, 1948, *pl. 503*). The abortive flowers and cupules are shown in FIGURE 107. Any one of the three flowers in a cymule can mature into a fruit. The upper cymule in FIGURE 107 shows the matured cupule of the central flower (the nut is removed to show the scar) subtended by two abortive lateral flowers; the lower cymule has one abortive and one fertile lateral flower and an abortive central flower. Occasionally, more than one flower matures a nut.

Although the cupular scales of *Lithocarpus scortechinii* are hidden by the bracteoles at anthesis (FIGURE 76), they quickly become prominent (FIGURE 77); by cupular maturity they are long and reflexed (Camus, 1948, *pl. 442*). The mature cupule covers much less than half of the nut. There are one primary and two distinct lateral bracteoles below the one-flowered cymule, and a ring of barely connate bracteoles above that (FIGURE 76). When the cupular scales enlarge, the ring of bracteoles is not readily distinguishable from the scales (FIGURE 77).



FIGURES 93–100. 93, *Lithocarpus densiflora:* segment near spike tip at anthesis, upper 4 cymules staminate, with 3 to 5 flowers and 5 to 7 bracteoles (not all visible here), pistillate cymules with 1 flower and 1 bracteole. 94–96, *L. soleriana:* 94, segment of staminate spike with 1- and 3-flowered cymules, 2 with flowers removed to show numerous bracteoles; 95, segment of pistillate spike at anthesis, showing 1-flowered cymules, each with 1 bracteole, cupular scales prominent; 96, mature cupule covering about half of nut, lamellae somewhat scaly. 97–100, *L. harmandii:* 97, 98, segments of pistillate

As in *Lithocarpus scortechinii* and other species, the mature cupule of the only American member of the genus, *L. densiflora,* covers little of the nut and is thickly invested with rather long, often recurved scales (Camus, 1948, *pl. 444*). The cymules are one-flowered and are subtended by a large primary bracteole (FIGURE 93); above this is a ring of slightly overlapping bracteoles that enclose the cupular scales, which are evident at anthesis (FIGURE 93).

The one-flowered pistillate cymules of *Lithocarpus sabulicola* have three bracteoles, one primary and two secondary, and there is a ring of strongly connate bracteoles that surrounds the remainder of the cymule. The ring does not entirely conceal the cupular scales at anthesis (FIGURE 83). At maturity the nut projects well beyond the scaly cupule (Camus, 1948, *pl. 464*).

The cymule bracteoles of *Lithocarpus dealbata* are not clearly distinguishable from the cupular scales. Although the primary bracteole is easily observed, the secondary ones are less so (FIGURE 88). Beyond them is a series of structures that are not clearly bracteoles or scales. The cupule encloses most of the nut at maturity, and it is invested with concentric rows of widely spaced, appressed, slightly elongate scales (Camus, 1948, *pls. 450, 451*).

SUBGENUS PSEUDOCASTANOPSIS. The cymules of *Lithocarpus fissa* subsp. *fissa* are one-flowered, and each has one bracteole (FIGURE 109). At anthesis the cupular scales and lamellae are obscured, but they are evident at maturity, at which time the cupule dehisces and the nut emerges (FIGURES 110, 111).

THE STAMINATE CYMULES

The staminate cymules are borne on staminate spikes, as well as above and below the pistillate cymules on mixed-sex spikes (Kaul & Abbe, 1984). On the latter spikes there are sometimes a few cymules that bear both staminate and pistillate flowers at the area of transition from entirely pistillate to entirely staminate cymules. The flowers in that area may be perfect, while those away from it are imperfect. Such transitional conditions are especially evident in species with multi-flowered cymules.

The staminate cymules are subtended by one or more bracteoles whose number and arrangement are the same as or different from those of the pistillate cymules of the same species. Often there are more bracteoles subtending the staminate than the pistillate cymules (see TABLE).

FIGURES 1 and 11 show the one-flowered staminate cymules of *Lithocarpus turbinata* and *L. pulchra* on the rachis beyond the pistillate cymules. Each staminate cymule has one long primary and two shorter secondary bracteoles, a condition often found in one-flowered staminate cymules in other subgenera. However, by contrast, the one-flowered cymules of *L. beccariana* (FIGURE 5) have only a primary bracteole. The situation is more complex in *L. hender-*

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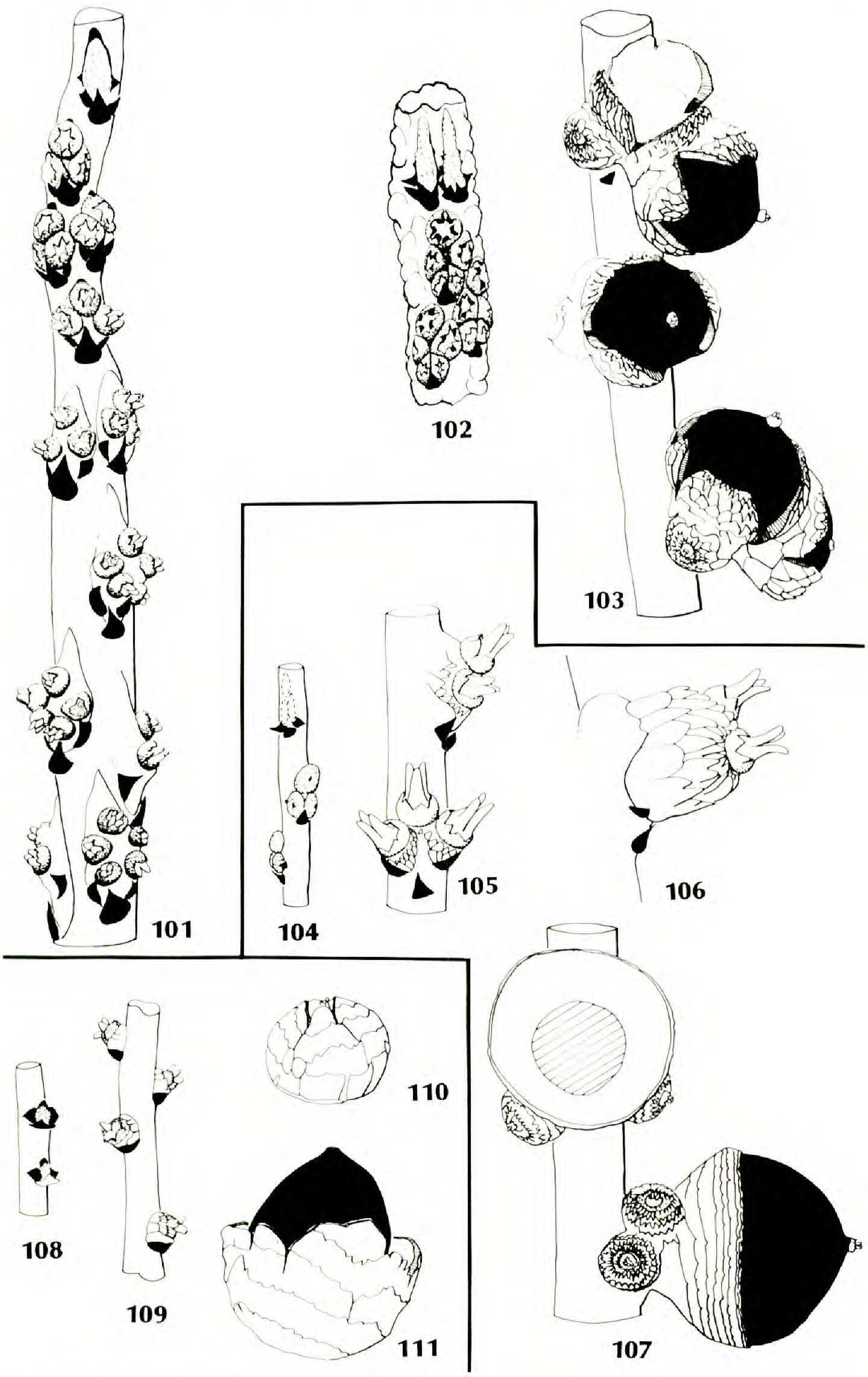
spikes at and shortly after anthesis, respectively, cymules 3- to 7-flowered, each with 1 prominent bracteole, well-developed staminodia present in flowers of uppermost cymules of FIGURE 97; 99, segment of staminate spike just before anthesis, cymules 7-flowered, each 3-bracteolate; 100, mature cupule and nut, each scale borne on enation. Figures 96, 99, 100, × 2; all others, × 4.



FIGURES 101–111. 101–103, *Lithocarpus elegans:* 101, segment near tip of androgynous spike at anthesis, upper 4 cymules staminate, uppermost with all 3 flowers removed to show bracteoles, pistillate cymules 3- to 5-flowered, each with 3 bracteoles and raised upon buttress; 102, segment of staminate spike at anthesis, 5-flowered cymules subtended by numerous bracteoles, upper 2 cymules with flowers removed; 103, mature, fruit-bearing pistillate spike, 1 cupule split and with parts fallen away, each cymule with 1 abortive flower and cupule. 104–107, *L. wallichiana:* 104, segment of staminate spike nearing anthesis, each cymule with 3 flowers and 3 bracteoles; 105, segment of pistillate spike at anthesis, each cymule with 3 flowers and 3 bracteoles, cupular scales evident; 106, pistillate cymule after anthesis; 107, mature cymules, each with 2 abortive flowers and cupules, mature cupule covering about half of nut and barely scaly. 108–111, *L.*

soniana (FIGURE 6): above the primary bracteole there is a series of low, basally connate bracteoles that encircle the entire cymule, just as they do in the pistillate cymules of that species. In all these species the bracteole pattern is the same in staminate and pistillate cymules.

The one- and three-flowered staminate cymules of *Lithocarpus amygdalifolia* and *L. nantoensis* (FIGURES 14, 15) have five bracteoles, with the primary always the largest. The five-flowered staminate cymules of *L. truncata* usually have seven bracteoles (FIGURE 17). The quaternary pair extends completely over the distal end of the cymule (not visible in figures).

In the three species illustrated from subg. *Gymnobalanus*, the staminate cymules are one- and three-flowered and three-bracteolate, and three-flowered and five-bracteolate (FIGURES 18, 22, 24).

In the large subgenus *Cyclobalanus* the bracteoles of the staminate cymules range from three to seven or more per cymule. A complex example is shown for *Lithocarpus lampadaria* in FIGURE 29. The staminate cymules are mostly five-flowered, and there is an elongate primary bracteole below each one. Above it, in pairs, are six additional bracteoles, some overlapping and some not (FIGURE 29, top). Four of the flowers of the cymule have one or more bracteoles beside them, but the distal flower does not. The bracteole pattern of the pistillate cupule is likewise complex (FIGURE 30).

Simpler bracteole patterns exist in *Lithocarpus reinwardtii*, where both the one- and the three-flowered staminate cymules have three bracteoles (FIGURE 36), as do some of the pistillate cymules (FIGURE 37). In *L. macphailii* the three-flowered staminate cymules have five bracteoles, and the pistillate cymules have that many or more (FIGURES 48–51). The simplest case is that of *L. neorobinsonii* (FIGURE 58), in which the staminate and pistillate cymules both have one flower and three bracteoles.

The bracteole pattern is somewhat complex in *Lithocarpus pattaniensis* because, although the cymules are always one-flowered, there are three or sometimes more bracteoles present, even on the same specimen (FIGURE 62). When the single flower is removed from the bracteoles, as in the upper two cymules in FIGURE 62, it can be seen that the secondary bracteoles are slightly confluent above the cymule, where they form a point that suggests another, reduced bracteole. Furthermore, within that encircling series of bracteoles there is sometimes a second set of four (two to six) tiny ones that suggest a rudimentary cupule (FIGURE 62, uppermost cymule).

The largest subgenus, *Pasania*, also has a great range of bracteole patterns in the staminate cymules. Some three-flowered cymules have but one bracteole (e.g., in *Lithocarpus garrettiana*, FIGURE 78), and some have three bracteoles (e.g., in *L. lucida*, FIGURE 25; *L. wrayi*, FIGURE 72; *L. hancei*, FIGURE 85; and *L. wallichiana*, FIGURE 104). Some cymules with five or more flowers also have

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fissa: 108, 109, segments of staminate and pistillate spikes at anthesis, each cymule with 1 flower, staminate with 3 or more bracteoles, pistillate with 1; 110, cupule nearing maturity and showing early signs of dehiscence; 111, mature, dehisced cupule revealing part of nut, lamellae prominent and barely scaly. Figures 103, 107, 110, 111, × 2; all others, × 4.

only three bracteoles (e.g., in *L. harmandii*, FIGURE 99), but so do some one-flowered cymules (e.g., in *L. wrayi*, FIGURE 73; *L. sabulicola*, FIGURE 82; *L. hancei*, FIGURE 84).

Complex bracteole patterns in the staminate cymules of subg. *Pasania* are illustrated here by seven species. *Lithocarpus scortechinii* (FIGURE 75), *L. harlandii* (FIGURE 81), *L. dealbata* (FIGURE 89), *L. soleriana* (FIGURE 94), and *L. elegans* (FIGURES 101, 102) illustrate a common arrangement: an identifiable primary bracteole and usually an identifiable pair of secondary ones. Beyond these three bracteoles is a series of smaller, sometimes irregular ones that are not always obviously paired. At the distal end of the cymule, the bracteoles are reduced and apparently fused; they usually surmount the cymule. Such complexity occurs in these species in one-, three-, and multi-flowered cymules, as shown in the figures. The three- and five-flowered staminate cymules of *L. densiflora* have five and seven bracteoles, respectively.

The most complex staminate bracteole pattern among the species studied is that of *Lithocarpus fenestrata*. In addition to having a series of complex bracteoles similar to those of the species discussed in the preceding paragraph, each flower is subtended by a whorl of small bracteoles that suggests a rudimentary cupule (FIGURE 80, upper two cymules, the small bracteoles not darkened).

Lithocarpus fissa, of subg. *Pseudocastanopsis*, has one-flowered staminate cymules, each with four subtending bracteoles, the fourth one located at the distal end of the cymule (FIGURE 108).

DISCUSSION

Some aspects of the bracteole patterns and the floral arrangement support the interpretation that the groups of flowers provisionally called cymules are actually that. Evidence is provided by the sequence of opening of the flowers in both staminate and pistillate cymules. In every instance the distal flower opens first, with the subjacent pair next, and the lowest pair last (i.e., the sequence is strictly basipetal within the cymule). Where more than five flowers are present in a cymule, the sequence of opening beyond the fifth flower is also generally basipetal, but the pattern is less obvious.

The primary bracteole and the paired secondary, tertiary, and subsequent bracteoles, as well as the absence of a bracteole immediately below the central flower, all suggest a condensed cyme. When the cymule has a single flower, sometimes one and sometimes three or more bracteoles subtend it. Where the number of bracteoles exceeds the number of flowers subtended, it is possible that each excess bracteole represents the single bracteole subtending a lost flower or branch of a complex, now-condensed branching system.

The bracteoles subtending the pistillate cymules are undoubtedly homologous with the cupular scales above them. The bracteoles merely represent the lowest bracteoles of the condensed branching system, while the scales are the bracteoles of the branches whose phylogenetic condensation formed the cupule. Some evolutionary increase in scale number could have occurred after sterilization of bracteoles and while the cupule was evolving.

Fey and Endress (1983) interpreted the fagaceous cupule as a complex, cymose branching system with shortened, united axes and with persistent bracteoles that form the cupular scales. They showed that, at least in earlier ontogenetic stages, the scales are regularly arranged in a pattern suggesting that of branched cymes. The subtending bracteoles discussed in this paper are then merely the lowest bracteoles of the much-reduced cymose system (cf. Fey & Endress, 1983, *fig. 21*). In many pistillate cymules the subtending bracteoles intergrade with the cupular scales, as would be expected with this interpretation.

In every instance where the ontogeny has been observed, the cupular scales are present at anthesis (but are sometimes obscured by the bracteoles). They may persist and even enlarge with the cupule, fully investing it at maturity, as in many species of subg. *Pasania.* In extreme cases (e.g., *Lithocarpus garrettiana,* FIGURE 91) the scales elongate greatly and the cupule becomes coarsely hirsute. They may also persist without enlarging, so that the mature cupule has obvious but small and often widely spaced scales, as in many species of subgenera *Lithocarpus, Synaedrys,* and *Gymnobalanus* and in some species of subg. *Cyclobalanus.* The extreme condition is seen especially in the last subgenus, where in many species the scales are lost during ontogeny because they either fall from the cupule or become ruptured during cupular expansion. Such mature cupules essentially lack scales, consisting of massively enlarged axial tissue of the cupule. The morphological nature of this axial tissue is yet to be defined, however.

Special conditions exist in subg. *Synaedrys* and in a few species of other subgenera. For example, in *Lithocarpus cornea* of subg. *Synaedrys* (FIGURE 10), the scales enlarge with the cupule and become totally adnate to it so that at maturity the cupule is mostly covered by them. In *L. pulchra* of the same subgenus (FIGURE 13), the scales or scale tips become elevated on tubercles, which completely cover the cupule. The morphological nature of these tubercles is unknown.

Soepadmo (1970) studied the vascular anatomy of the cupule of *Lithocarpus* and found the same vascular organization as that in the *Quercus* cupule (Kaul, 1985, *fig. 36*). In pistillate cymules that mature more than one fruit, the cupules usually become connate laterally. When this occurs, the vascular systems of the individual cupules remain distinct in the fused, "interseminal" cupular walls. The more or less regular patterns of dichotomous branching of the cupular vascular bundles, ultimately serving each scale with a vascular trace, could be interpreted as evidence of the cymose history of the cupule (Kaul, 1985), but the extreme condensation in the cupule and the lack of intermediate forms make any interpretation of vascular evidence tentative.

The function of the cupule is probably protection, first of the flower and later of the fruit, and in this aspect its evolutionary history resembles that postulated for the inferior ovary. However, the ovary of *Lithocarpus* is inferior and the ovary wall at anthesis is not especially thick, although it becomes so with maturity. Additional, often formidable, protection is possibly provided by the cupule from anthesis onward, not only by the scales but also by the large amounts of tannins, crystals, and sclereids present.

In all species the cupule provides complete coverage of the immature nut, but in many the maturing nut emerges from the cupule, by which time its own pericarp is very strong.

As in *Quercus*, effective dissemination of the fruits of *Lithocarpus* requires animals (but see Boucher, 1981). Monkeys, squirrels, and similar mammals are known to be especially important in burying the nuts (Camus, 1952–1954; pers. obs.), which have hypogeal germination. Some nuts are, of course, eaten by those animals, but many are buried and not exhumed.

The real or apparent dehiscence of some cupules recalls the more obvious dehiscence of the cupules of *Castanea* and *Castanopsis*. The pattern is regular in some species of *Lithocarpus* (e.g., *L. encleisacarpa, L. garrettiana*) but irregular in others. Correspondence of dehiscence lines to sutures between valves is unknown for *Lithocarpus* but is understood for some other fagaceous genera.

Some mature cupules of *Lithocarpus* bear abortive pistillate flowers at various sites (see, for example, FIGURES 3, 8, 10). Often it is clear that these abortive flowers are merely other flowers of the cymule that have been elevated somewhat by the overwhelming growth of the cupule of the fertilized flower (FIGURES 8, 10, 35). In other instances such abortive flowers have probably actually formed upon the cupule itself from latent floral primordia of the ancestral, now-condensed, cymose branching system that produced the cupule (see FIGURE 3). Fey and Endress (1983) stated that apparently adventitious staminate flowers upon the cupule of *Fagus sylvatica* L., as reported by Cole (1923), are not unexpected if each cupular valve is interpreted as a modified branching system. That concept also seems valid for the presence of pistillate flowers on the upper regions of mature cupules.

In such a large genus as *Lithocarpus*, there has undoubtedly been substantial adaptive radiation, parallelism, and convergence leading to a plethora of patterns of reproductive structure. There is very little published information that relates reproductive structure in the genus to habitat or pollination specializations, making interpretations of structure/function relationships difficult.

The homology of staminate with pistillate cymules, as suggested by Kaul and Kaul (1981), is corroborated by the evidence presented here. Not only do those cymules have similar bracteole patterns in general, but they also occupy interchangeable sites in some spikes. In a few staminate cymules, such as those of *Lithocarpus fenestrata* and *L. pattaniensis*, there is a set of bracteoles interior to the main ones. These are probably additional residual bracteoles of a condensed branching system and may represent a rudimentary system of cupular scales in the staminate cymules, perhaps fully homologous with the cupular scales of the pistillate cymules. In some cymules the flowers are both staminate and pistillate, or perfect, or perfect and imperfect (sometimes all of these on a single spike), indicating that separation of the sexes is not complete at flower and cymule levels. In *Quercus*, by contrast, the functional sexes are strictly separated into different spikes (except in obviously aberrant specimens), but the pistillate flowers often have well-developed staminodia, especially in the tropical species (Kaul, 1985). Neither *Quercus* nor *Lithocarpus* is dioecious.

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